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The Leaping Behaviour of Salmon and Trout at Falls and Obstructions

By T. A. STUART, B.Sc.

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By T. A. STUART, B.Sc.
Freshwater Fisheries Laboratory, Pitlochry

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1962

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The Leaping Behaviour of Salmon and Trout at Falls and Obstructions

INTRODUCTION

The jumping or leaping activity of salmon and trout on passage over waterfalls and weirs on their way from the sea to their spawning grounds is, and has been for centuries, of perennial interest to many observers whose sole interest resides only in the spectacle so provided. Others, particularly those concerned with the preservation of the fisheries, tend to view such obstacles to smooth passage upstream with disfavour and endeavour at every opportunity to modify them.

Intended originally to alleviate the difficulties of passage over low weirs and mill dams (and to comply with the laws on obstructions), various types of passes or fishways were constructed, some of which were successful but a relatively large number were either not successful or very moderately so (Calderwood, 1926).

In recent years however, the impoundment by high dams of the water of salmon rivers for the purpose of hydro-electric development etc., has created major obstacles to the free movement of migratory fish and interest in the design of fish passes has correspondingly increased. Fish passes of diverse type are now in use, and are being constructed, but only in a very few cases do they differ in principle from the earlier designs. One of the most common of recent types of fish pass consists of a flight of stepped pools and is referred to as a 'fish ladder'. Various modifications of these pools exist, chiefly concerned with the manner in which water flows from one to the other—by means of notches and baffles of diverse design or by submerged orifices—the aims being (*a*) economy of water, and (*b*) the avoidance of high velocity and excessive turbulence in the pools to meet the requirement that 'the fish should be able to swim through the pass without undue effort' (R.C.F.P.,* 1942).

The need to avoid high velocities seems at first sight to be obvious, the avoidance of turbulence being related to the well-established fact that salmon do not readily leap at an obstacle from 'white water', i.e. super aerated water, until the temperature of the water reaches about 42°F (Calderwood, 1926; Menzies, 1934). Such 'white water' constitutes a barrier that obstructs or delays the ascent of the valuable 'spring' salmon which enter the rivers during the colder months of the year; the condition, of course, obtains in some natural waterfalls as well as in artificial ones.

It has been suggested (Calderwood, 1926; Menzies, 1934; Pryce-Tannatt, 1938) that this effect of super aerated water is due to the reduction of propulsive power of the fish tail in a medium composed largely of foam, though the Report of the Committee on Fish Passes (1942) states that further evidence is desirable. However, Smetana (1935) found that the specific weight of the water in the aerated roller of a standing wave was materially less than that of plain water and in this less dense medium there is bound to be some loss of propulsive power. However that may be, it will be shown below (p. 31) that the presence of 'white water' is symptomatic of hydraulic conditions which block the stimulus to jump although the effort demanded by the height of the obstacle may be well within the powers of the fish.

It is a remarkable fact that, although the leaping behaviour of fishes is so well known in relation to obstructions, to their reactions as the sport of anglers and to their frequent, spontaneous and apparently purposeless leaps from more or less static water, this spectacular propensity appears to have received little, if any, attention from serious investigators. We can indeed trace the origin of present day beliefs

*Report of the Committee on Fish-passes.

(which appear to have influenced the design of modern fish passes in a negative manner) to flights of poetic fancy as in the 'Poly-olbion' of Michael Drayton (1612):

> 'Here, when the labouring fish does at the foot (of the fall) arrive,
> And finds that by his strength he does but vainly strive;
> His tail takes in his mouth, and bending like a bow
> That's to full compass drawn, aloft himself doth throw.'

Two centuries later we find in Williamson (1822) (quoted by Sparrow, 1923) the idea surviving, with elaborations: 'The manner in which the salmon leaps is singular. It descends deep into the water, and turning its head towards the fall, makes upwards with all its force; but as it reaches the surface brings its tail up to its mouth, and using it as a spring, casts itself towards the height to be surmounted. I have frequently seen them in this manner ascend about ten or eleven feet, but I have read of their leaping much higher.'

In recent years the 'tail in mouth' technique has been discredited but the *reculer pour mieux sauter* concept persists without benefit of positive evidence. Thus: 'In order to leap a fish must have a deep water take off' (Calderwood, 1926); 'A sheer fall of 6 ft is probably, to all intents and purposes, about the maximum practicable for the great majority of salmon, even under the most favourable conditions, among the latter of which must be included plenty of room and depth below to enable the fish to develop the necessary velocity.' (Pryce-Tannatt, 1938); 'Fish can, as a last resource, cross some obstacles by leaping, provided they have a sufficient length of clear run in water of adequate depth' (R.C.F.P. 1942).

These unsupported statements (which, it will be noted, implicitly attribute to the fish a teleological behaviour) have undoubtedly been responsible for present day designs which seek to eliminate waterfalls almost completely. On the steep inclined ramp that formed the basis of the earliest fishway, up which fish were expected to swim and which proved impracticable in most cases owing to the high velocities attained by the 'shooting' water, modifications were introduced in the shape of checks, stops or baffles to reduce the velocity. But these obstacles transformed the rapidly gliding water into a turbulent, white foaming torrent which was, to the early running fish in particular, an equally impassable barrier.

It is not proposed to describe the evolution of fish passes here. The subject has been very thoroughly dealt with by the authors cited above, all of whom are agreed that the perfect fish pass has not yet been designed. It will suffice to note that modern designs of fish ladders reflect a compromise between the chute and natural fall of water in a river bed. Examples show a wide diversity of slope and size of pool, and overall gradients ranging from about 1:6 to 1:17; in most cases, if not all, the rise between pools is not greater than 2 feet, to conform with the widely held view that the larger the pools, and the smaller the rise between them, the more efficient the pass will be (R.C.F.P., 1942). This leads, in some cases, to excessively long and costly ladders which must also turn in hair pin bends to bring the entrance close to the front of the dam in order that it may be readily located by the ascending fish.

The present investigation was undertaken primarily to study the behaviour of salmonids at waterfalls and artificial obstructions: in particular the purposive and directed movements reported by, among others, the authors quoted above, by means of which the fish was credited with an ability to estimate both the height of the jump and the length of 'run' necessary to attain a velocity sufficient to launch its body from the pool below to the requisite height.

At the outset it became quickly apparent that the leaping fish invariably commenced its jump from near the surface of the pool and never from the depths and its approach to the 'take off' point could only be described as relatively 'leisurely'. The approach was usually made from downstream with the body at an angle of between 20° and 30° to the surface of the pool and the head pointed downwards. Very often the tail broke the surface of the water during the approach.

LOCATION AND APPARATUS

Observations and experiments were conducted in the laboratory and in the field.

For the purpose of this work in the laboratory a channel $50 \times 1{\cdot}25 \times 1{\cdot}5$ ft was constructed in transparent 'Perspex' ($\frac{1}{4}$ in. thick) mounted on a girder of 'Dexion' slotted steel angle (Fig. 1). The channel was

divided into two parts, the upper part 30 ft long and the lower 20 ft. The upper channel was mounted 20 in. above the lower and water connexion was maintained by a 'fish ladder', constructed of the same material, of slightly narrower dimensions which permitted its suspension within the walls of the lower channel. The ladder unit comprised three stepped pools with an overall gradient of 1:3 and was detachable. The girder carrying the upper channel was mounted on a pedestal about 10 ft from the lower end by means of a 1 in. diameter steel rod on which the whole assembly pivoted when the upper end

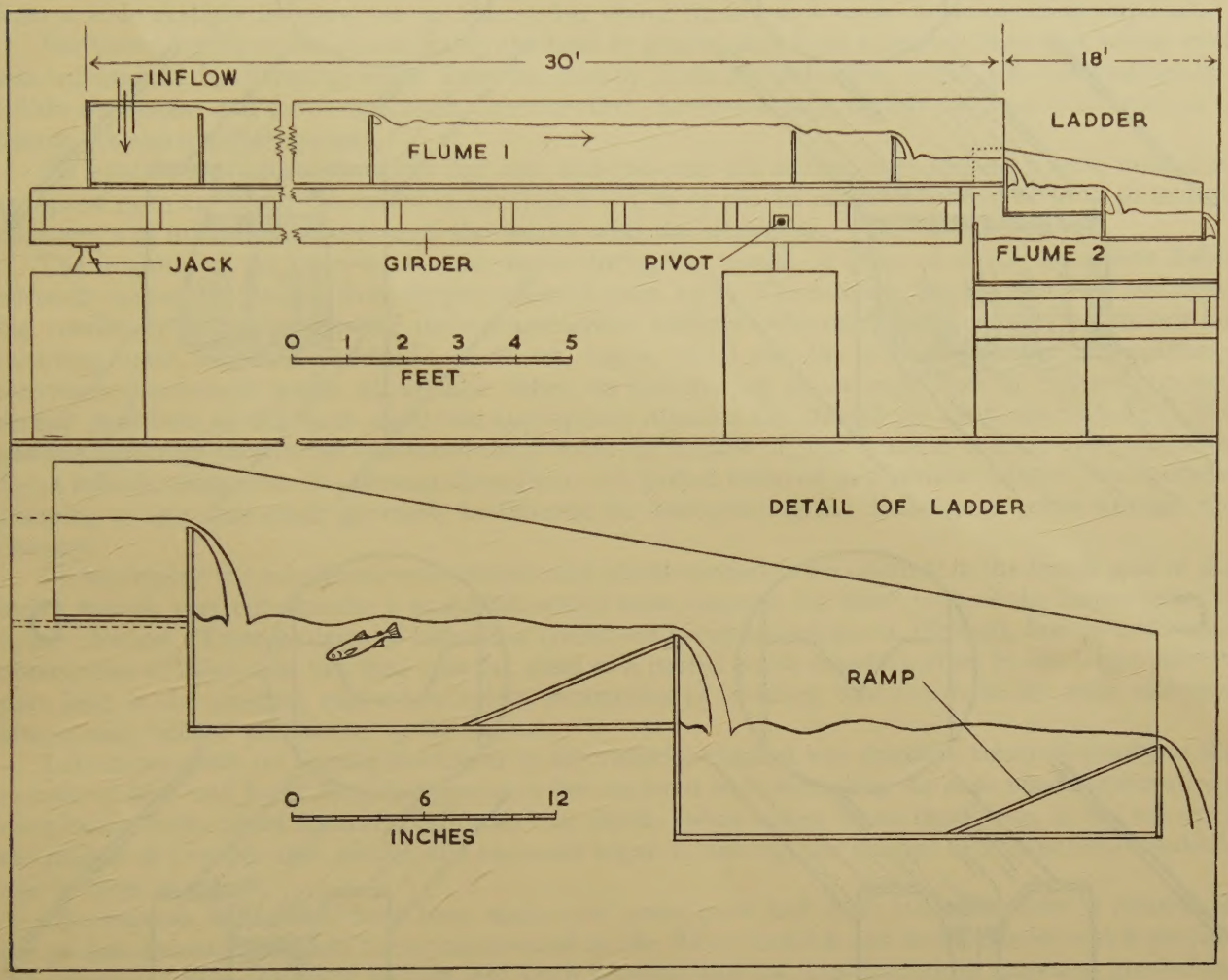

Fig. 1 Laboratory channels and detail of fish-ladder pools.

was raised or lowered by means of a hydraulic jack. Two screw jacks were used for final adjustment at the chosen gradient. Provision was also made in the channels for the insertion of dams and spillways of various sizes. In this manner the open channels could be converted into a series of falls and pools, the respective heights and depths being adjustable by using dams of different heights and/or increasing or decreasing the overall gradient. The faces of the dams and the bases of the channels were rendered opaque by painting with a bitumen compound. The bases of the channels were also roughened by adding a layer of coarse sand to the still tacky coat. The dams or weirs were constructed of $\frac{1}{4}$ in. 'Perspex' and consisted of a single sheet of the material which slid into grooves on each side of the channel and fitted closely to the base. Several forms were employed, these being classified as rectangular, triangular and trapezoidal, according to the shape of the opening through which the water passes. The rectangular weirs are further subdivided into (*a*) weirs with side plates which limit the length of the crest to less

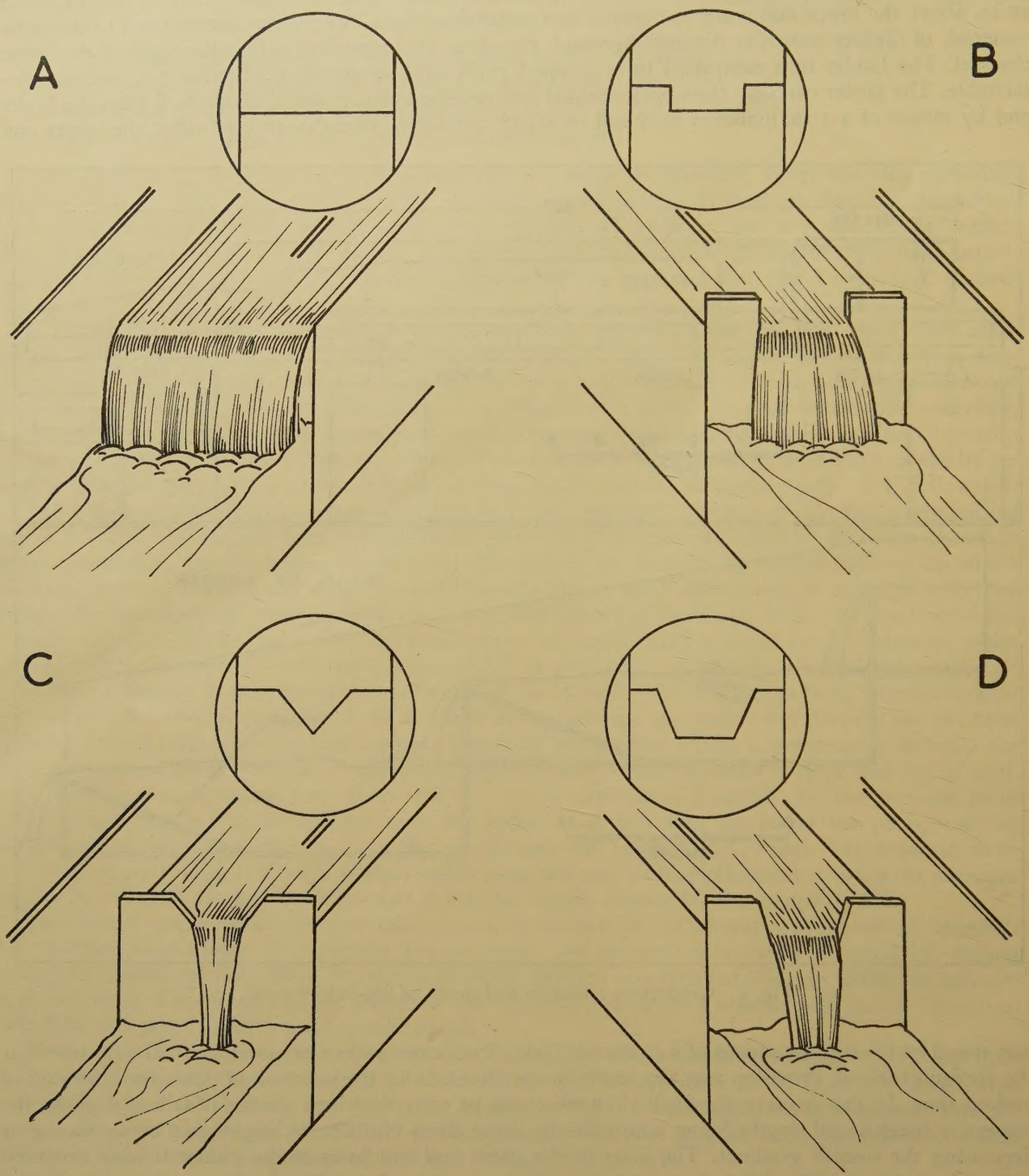

Fig. 2 Weirs and notches: A, broad spillway, B, rectangular notch, C, triangular notch, D, trapezoidal notch.

than the width of the channel, and (*b*) weirs whose side walls are formed by the vertical sides of the channel. Triangular weirs are in the form of a V-notch and the trapezoidal may be considered as a combination of triangular and rectangular weirs (Fig. 2).

A light coloured brick wall provided a background for the length of the channel and a removable side wall of plywood was placed on the front. For photographic purposes, white paper was substituted for the brick wall background, but no difference in the behaviour of leaping fish was observed with either background. The channels were brightly illuminated throughout their length by natural light from a wide skylight between two and three feet above them which could be screened as required.

The water supply to the channels was obtained by gravity flow from a large storage tank whose level was maintained by pumping water from the nearby Loch Faskally. The water was not recirculated within the system and the temperature, uncontrolled, fluctuated only slightly between 10°C and 12°C during the experimental period.

For experimental purposes about 150 one- and two-year-old salmon parr and trout were utilised in groups of 15 to 20. These fish varied in size from 6 cm. to 15 cm. In addition, a shoal of 30 to 40 mature minnows was utilised separately and also jointly with the salmonids.

The majority of the observations was made during the month of May, at which time these fishes normally ascend the streams from deeper waters (Stuart, 1957). The minnows at this time were in breeding condition, the males showing their characteristic brilliant colouring. The necessary conditions for spawning were, however, withheld (see Stuart, 1953a, 1954) and the minnows persisted in upstream movement for several weeks. All of these fishes, on introduction to the experimental channels, moved readily upstream at this time under the appropriate stimulus and cleared the obstacles with ease. The positive upstream motivation continued until about the middle of June when it became more sporadic. Fresh introductions from the streams throughout this period behaved in a similar manner, but sporadic jumping at any time could generally be induced by manipulating the discharge of water through the channel.

By September the movement was reversed and all fish tended to accumulate in the lowest pool of the series, though very occasionally a single fish would move through the three pools of the ladder into the upper channel. These patterns of behaviour confirmed previous findings in the field, but an additional observation of interest at this time was the onset of a partial smolt transformation in the larger salmon parr held in the channel, and a concurrent resumption of breeding colouration in the male minnows after a long 'eclipse' period during the summer.

Laboratory work on leaping behaviour in the artificial channel was therefore confined chiefly to the months of May and June. By July however, a few sea trout were ascending the river where observations were being made under natural conditions, but, chiefly owing to low water conditions, it was not until the middle of October that salmon and sea trout began to attempt the passage of obstructions regularly and in large numbers.

Observations in the field have been made over many years but more intensive study in relation to the present investigations has been concentrated on the River Endrick and its tributaries which provide the principal volume of water flowing into Loch Lomond and the most important spawning ground for salmon and sea trout in the area. The Endrick, after leaving its peaty sources in the Fintry and Gargunnock Hills, runs in a westerly direction to Loch Lomond through more fertile land and for the main part of its course flows over rocks of the Lower Old Red Sandstone. Below Gartness, in the lower middle reaches, there is a serious obstacle to the passage of migratory fish at the falls of the Pot of Gartness whose downstream dipping rocks, formed of the harder layers of sandstone which project as crags on the banks of the river, make the relatively low falls of peculiar difficulty to salmon. About three quarters of a mile above the Pot, lesser falls plus a broken dam dyke close upstream, constitute another hazard to the fish, but not a serious obstacle except in low water.

Owing to the irregular nature of these falls and the 'potholed' condition of the rocks it was not practicable to measure discharges or velocities. The lack of uniformity was, however, of special advantage to this study. At low water levels the flow over the falls is concentrated mainly in a small area close to the left bank, but with rising water levels other falls are formed which one by one extend across to the right bank and all converge into the same deep pool. As a result, at most river levels between very low

and very high, the waiting fish can attempt the passage at a fall whose discharge may attract them more than another though, as will be shown below (p. 24), all available paths are of equal difficulty. With rising and falling levels the continual variations in conditions of discharge and velocity in these unequal falls (which, as mentioned above, enter the same pool concurrently or successively) provided many desirable experimental situations which could not have been engineered at this site. In some of the smaller tributaries however, it was perfectly feasible to manipulate the dimensions of a fall or the characteristics of the pool below and to observe the effects, during spawning runs, on sea trout and brown trout.

LABORATORY EXPERIMENTS AND OBSERVATIONS

In these experiments, salmon parr and trout aged 1+ and 2+ years were, at various times, used separately and jointly. Some of the trout derived from the River Endrick and possibly included sea trout as well as brown trout. The salmon parr and the majority of brown trout were taken from streams near the laboratory. As no differences in behaviour or performance relevant to these experiments were observed at any time between the two species, or between individuals within the size range (6-15 cm.) used in the experiments, the following remarks apply generally. Slight differences were apparent in the behaviour of the minnows and these will be discussed at the appropriate place.

Rate of Flow and Upstream Movement

The channels were first set up with ladder and weirs in position on a level base and the water supply was reduced to the minimum necessary to keep the pools filled without overflow. The weirs and ladder assembly were not sealed in any way and their relative water-tightness was obtained by close fitting. There was inevitably a slight leakage which was not considered to affect the experiments in any way as the orientation of the fish when introduced did not indicate the presence of any directional stimulus. During longer experiments the slight leakage was further reduced as deposits of fine silt accumulated. In this manner, five pools, each about eight feet long, were obtained, excluding those of the ladder; the level of successive pools decreased by about four inches and the depths of the pools varied from fifteen to seven inches.

Salmon, trout and minnows were then introduced to each pool in groups of 20. At different times the three species were used separately or in mixed groups of approximately equal numbers. Under these more or less static water conditions no 'upstream' movement took place and the fish were distributed at random over the base of the pool. No attempts either were made by the fish to move 'downstream' to a lower pool, although no emergent barrier to their progress in this direction was present. These conditions were repeated very often between other experiments in the course of this investigation with similar results. In all cases the fish behaved in a normal manner, the salmon and trout bullying each other (see p. 21), the minnows swimming peaceably in a shoal and all feeding regularly and well. The minnows, however, did not exhibit 'courting' behaviour and the males reverted to normal colouration.

The supply of water to the channel was then gently increased to a flow of 2 gals/min. so that the water just commenced to flow over the broad weir A as a thin film adhering to the vertical downstream face of the dam. Little apparent attention was paid to this flow by the fish, except when they were close to the face of the weir, although minnows appeared to be attracted by the occasional small air bubble carried beneath the surface of the pool.

The flow was further increased to 4 gals/min. without affecting the general disposition of the fish in the pool, but as all species approached closely to the weir they adopted a head down attitude with the long axis of the body at an angle of about 20° to the surface. Salmon and trout did no more than this though they tended to favour the upstream half of the pool, but the minnows showed a definite reaction to the new conditions. Singly, or in twos and threes, they approached the underwater face of the weir from all levels in the pool with head pointed downwards; just before they touched the weir they re-orientated suddenly to apply the belly to the face of the weir and, with head now pointing directly upwards and bodies closely applied to the underwater face of the weir, they swam *slowly* upwards

(Figs. 3, 4A). The vertical swimming movement was continued until their noses just penetrated the surface film of water when they broke away to resume normal orientation, then to repeat this behaviour.

Tests made with strong solutions of dye, applied just upstream from the crest of the weir while the minnows were performing, showed that the apron or 'nappe' of water flowing down the face of the weir continued to flow towards the bottom of the pool for a distance at least equal to the height of the weir above the surface without obvious dispersion or displacement. The minnows, therefore, throughout this experiment were orientated in a normal direction to the current, were attracted by the current and swam upstream, but failed to penetrate beyond the surface of the pool, most probably owing to their low velocity and as a result of the sudden loss of buoyancy at this point.

A progressive increase of flow to 12 gals/min. strengthened all aspects of this behaviour and brought positive reactions from the salmonids. It was found that with this weir (A) the flow could be increased to the above value with the nappe still adhering to the surface of the weir. As it approached this discharge however, any slight disturbance of the crest caused the nappe to spring out from the weir and take the characteristic form of the jet shown in Fig. 4B.

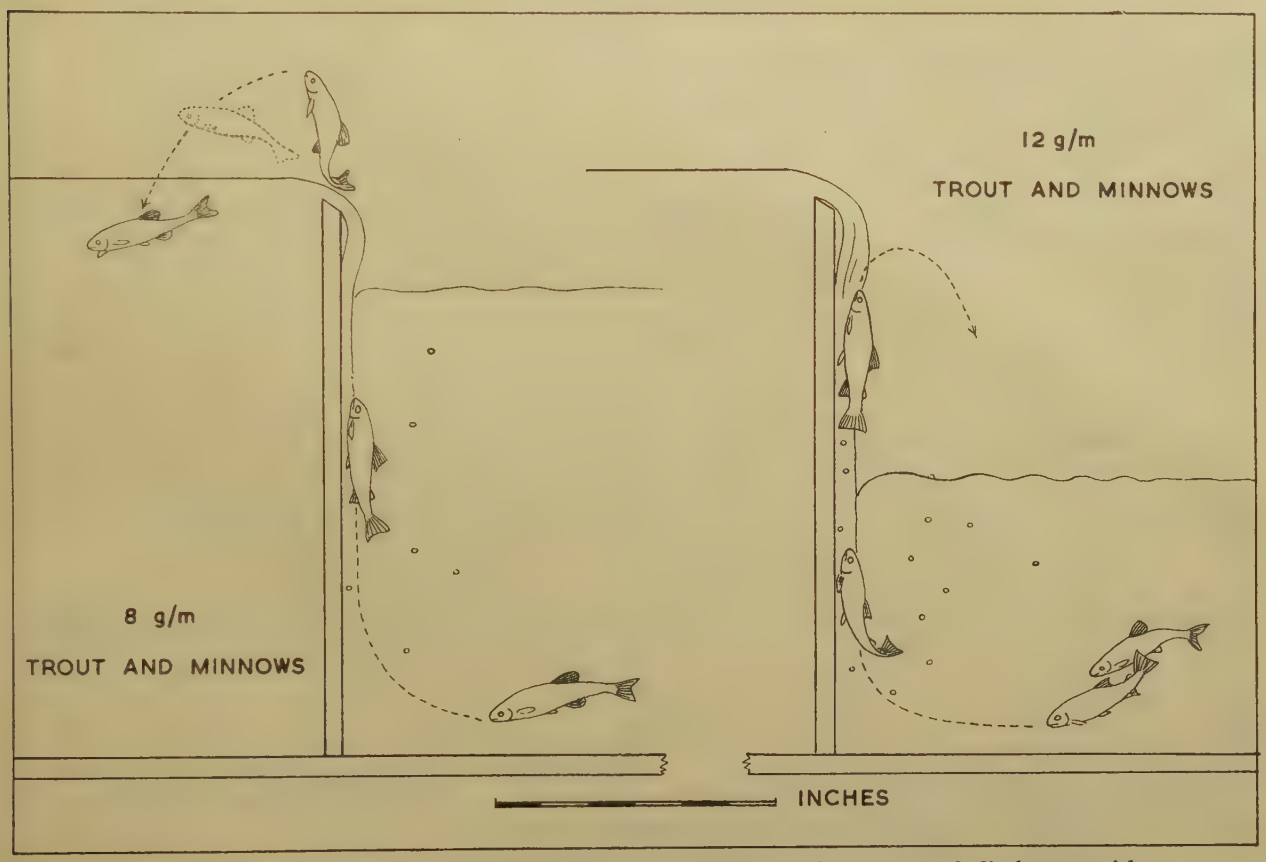

Fig. 3 Trout and minnows swimming up weir face at low rates of discharge with adherent nappe.

Before this point was reached the minnows behaved as before and were joined in similar behaviour by the salmonids when the flow attained a rate of about 8 gals/min. With increasing discharge and velocity down the face of the weir, however, their vertical swimming speeds paradoxically also became greater, with the result that when the fish broke the surface of the pool they were able to continue swimming up the adherent nappe for a second or so. This had the effect of taking the fish about three inches up the vertical face before they were swept back, and later, when the height of the weir was reduced to three inches, about one effort in ten (Table 1) placed the fish in the upstream pool (Fig. 3). Failures were almost certainly due to the perpendicular nature of the obstacle.

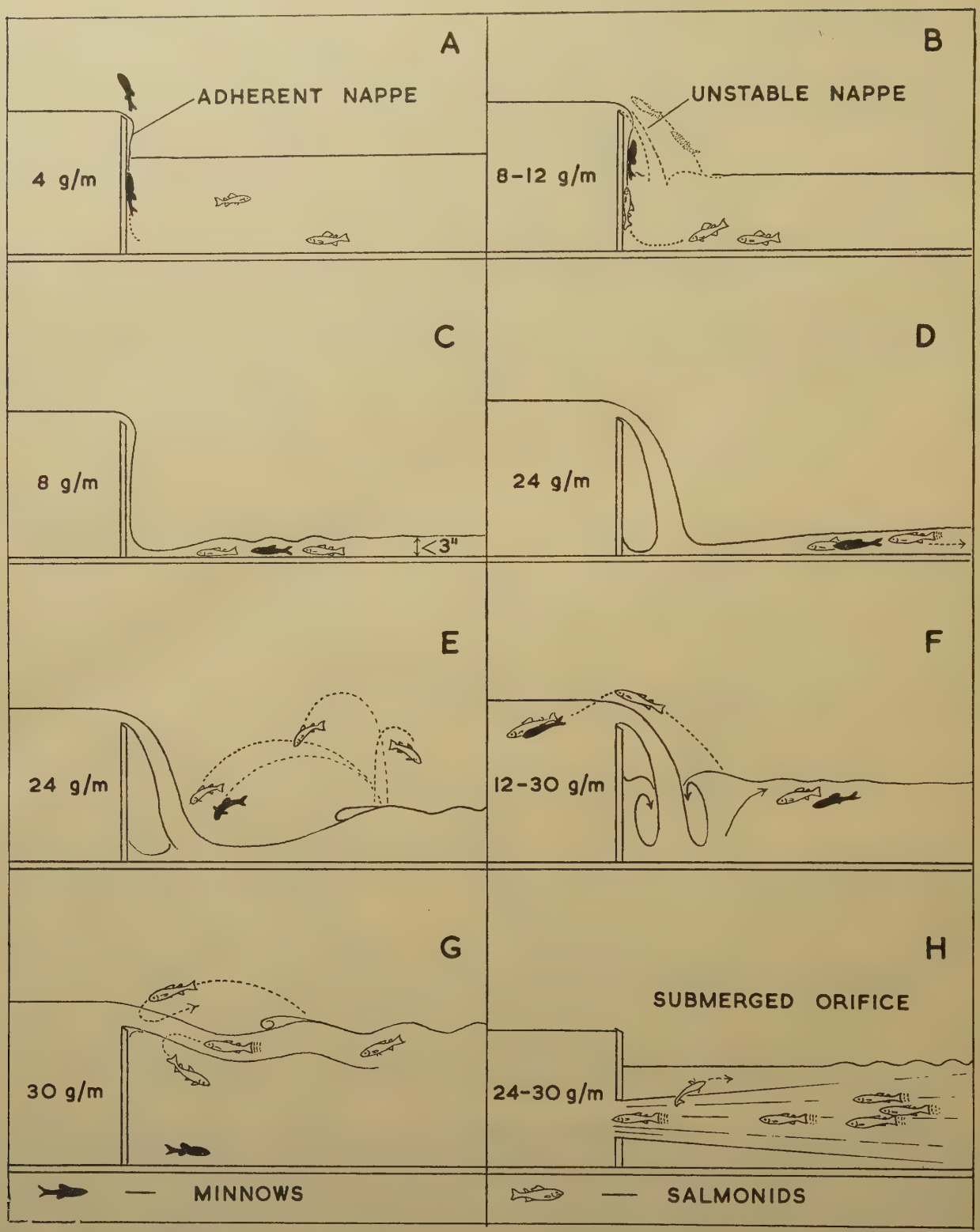

Fig. 4 The reactions of minnows, trout and salmon parr to different types of overfall at various rates of discharge and pool depths.

Minnows were by far the most active performers. Typical analyses of 20 consecutive efforts at the lower weir from a mixed group showed that, on the average, minnows may be expected to make the attempt, under these conditions, three times more often than the salmonids. Analyses of successful efforts using homogeneous groups however, showed that the salmonids were twice as good performers (Table 2).

It would appear from this experiment that the increased flow of water had an equal stimulatory effect on all three species, but the threshold of the reaction for swimming up the weir was lower for the minnows. It is just possible, however, that the concerted actions of the minnow shoal may have had its own stimulus for the individuals and so might account for the greater activity and the lower threshold. It did not occur to the writer to test this theory until the experiments were concluded and the response was waning, but throughout the summer months, whenever the fish were confined to the lower channel, solitary salmon and trout would often ascend through the whole system—but never a minnow. This question therefore requires further investigation. It was noted, however, that as activity increased with enhanced flow, the male minnows reassumed their spawning colouration.

Pool Depth

The possibilities of progression over the weir having been roughly demonstrated by the above experiment, the effect of pool depth below the weir height was now considered. Hitherto pool depth had exceeded weir height by from one to ten inches without noticeable effect and when the depth of the pool was reduced to three inches, still no differences were apparent. The rate of flow which first brought the salmonids into action, approximately 8 gals/min. was used for the following observations.

By using the hydraulic jack to alter the gradient it was possible to reduce the level of the pool beneath the weir by almost imperceptible degrees without interrupting the activity of the fish. When the level of the pool dropped below three inches it was observed that all approaches to the weir commenced from a position in the pool about 12 in. from the weir, whereas, before, no movement that could be described as 'purposeful' took place until the fish was close under the weir. The 'head down' attitude remained the same however, until the pool became too shallow, but it was seen that the fish now approached the weir along a path that lay near the bottom of the pool and only rarely at the surface (Figs. 3, 4C). It was thus found that the fish were not hindered in any way in their attempts on the weir (although few successful passages were now made owing to the increasing height of the weir relative to the surface of the pool) until the depth was reduced to three quarters of an inch at the foot of the weir. At this low level the majority of attempts by all species were made at the corners formed by the weir and the walls of the channel, though many fish first approached the weir from the middle of the channel. Attempts near the middle of the weir appeared to fail owing to the inability of the fish to assume the vertical position in the shallow water, and while still trying to swim forward they moved laterally to either corner. At no time during any of the experiments so far recorded did a fish leap from the pool to surmount the obstacle.

By repeating the previous tests with solutions of dye, it was shown that the current down the face of the weir, instead of dispersing before it reached the bottom of the pool, now continued to flow along the bottom of the channel and only became diffuse beyond the point where the fish began their positive forward movements towards the weir. Once again the importance of a directive current was demonstrated, but it was obvious that no benefit accrued to the fish under the above conditions. It was quite evident that, whereas in the deep water experiment the fish was able to reserve its energies until it was literally face to face with the obstacle, under the new conditions it was forced to begin the effort twelve inches downstream with no possibility of utilizing its momentum to assist the progression up the face of the weir. Had it been possible to increase the velocity of the current while retaining all the other factors, it would have been easy to attain a velocity that would have defeated the fish before it ever reached the weir. Such a situation did arise under two rather different sets of conditions, one of which will now be described.

In these experiments an increased flow approaching a value of 12 gals/min. caused the nappe to spring out from the crest of the weir and enter the pool a few inches downstream (Fig. 4B). At discharges of between 8 and 12 gals/min. the adherent nappe was very unstable and, instead of presenting a smooth surface downstream, its surface was striated. Under shallow water conditions with the pool about 2 inches

deep and the nappe adherent, some fish were able to negotiate, by swimming, the vertical weir. But as a fish passed the crest of the weir the disturbance would often cause the nappe to 'flick over' to the free condition with the result that no further attempts were made by the remaining fish to pass the obstacle. At the higher discharges, the impact of the jet on the base of the shallow pool resulted in high velocity currents, radiating from the point of contact, which proved, apparently, too strong for the fish and prevented them from reaching the falling water.

When the flow of water was increased to a rate of 24 gals/min. the nappe became permanently free, smooth and stable. In the shallow pool below, no fish could approach the falling water owing to the high velocity near the fall, although they persisted in their efforts for a considerable time. Also, as a result of the impact, the water in this region became superaerated (Fig. 4D).

The gradient of the channel was now slowly decreased, giving a corresponding increase in depth of the lower pool. As the pool deepened the fish were able to approach closer to the fall and when the depth at the foot of the weir reached $3\frac{1}{2}$ inches several fish began to leap out of the water—but at a distance of 12 to 14 inches from the weir (Fig. 4E). Although the fish were now able to approach (although with some difficulty) within three or four inches of the fall, few did so and no leaps took place at this close range. Many leaps appeared to be disorientated. A few were made towards the fall, the fish describing an arc which made contact with the pool again at the foot of the fall; a rare leap took a fish downstream, but the majority were almost vertical. Some of the latter leaps attained only a few inches in height but several fish succeeded in clearing the walls of the channel—a feat that entailed a clear leap of over 15 inches—about three times their own length, and which seemed quite remarkable at this time. Later, in a natural river, comparable fish were seen to make leaps of up to ten times their own length.

The use of dyes to determine the course of the current was now impracticable owing to the high velocity and turbulence, but as mentioned above, in the shallow water the impact of the fall entrained large quantities of air which, in the form of masses of fine bubbles, gave a good indication of the course of the currents. It was thus seen that the heavy jet of water on striking the shallow pool was deflected and continued virtually unchecked along the bottom for a distance of at least 12 inches, at which point a standing wave was formed with minor waves behind. In front of the crest of the standing wave a roller developed which advanced and retreated in the space of a few inches in an irregular fashion. The region from which the leaps originated was just behind this broad roller, i.e. near the crest of the standing wave (Fig. 4E).

It can be shown that at this place there is a rapid decrease in velocity accompanied by a corresponding loss in energy, conditions which, it may be reasonable to assume, the fish is equipped to distinguish.

Dynamics of Flow in Open Channels

When water passes over a weir the potential energy of the head of water is transformed to kinetic energy. The degree of rapidity of flow, or kineticity, depends on the channel conditions immediately downstream from the weir. If these conditions are such that the velocity increases, the depth of water decreases and it can be shown that the change in the depth of flow is equal to the head loss due to friction plus the increase in kinetic energy.

If the flow is rapid as it enters the lower channel, and the depth is increasing in the direction of flow, the flow will pass suddenly from the rapid state to the tranquil state and a hydraulic jump (or standing wave) will be formed as an almost vertical wall of water at the point where equilibrium is obtained. The energy loss in the hydraulic jump, when subtracted from the total specific energy on the upstream side of the wave, equals the total specific energy on the downstream side. Hydraulically, the hydraulic jump is similar to the sudden expansion of a jet in a closed pipe, where the rapid decrease in velocity is accompanied by a corresponding loss in energy (Linford, 1949).

In natural channels, the flow of water is always irregular or turbulent and at any given point the velocity is found to vary from moment to moment both in magnitude and direction. At points where the motion is steadiest variations amounting to 20% of the mean velocity will be found (Parker, 1925). Similar phenomena have also been noted in spillways and laboratory channels (R.C.F.P., 1942). As a result of these irregularities, disturbances take place in the channel which, reinforced perhaps by obstructions etc., take the form of surges which travel upstream as gravitational waves.

The speed of propagation of these small waves or surges is called the 'celerity', C, and is given as $C=\sqrt{gh}$, where g is the acceleration due to gravity and h the height of the wave.

The velocity, v, in a channel may be smaller or greater than $\sqrt{gh}$ and, depending on this, the flow will be 'shooting' (hypercritical) or slowly varying (infracritical). In the first case, a disturbance taking the shape of a gravity wave, or a surge, must travel upstream with an absolute velocity $\sqrt{gh}-v$. If however, $v=\sqrt{gh}$, the surge will become stationary and produce a standing wave, or hydraulic jump. This velocity is therefore called the 'critical' velocity (Leliavsky, 1955a).

It is clear therefore that if the velocity in a pool below a weir is above the critical (rapid flow) the depth will continue to decrease downstream. If, on the other hand, with increasing depth the velocity is below the critical (tranquil flow) a hydraulic jump is formed at the point of equilibrium. Should the depth further increase, the standing wave will approach the foot of the weir and, with depth increasing still further, will be eventually submerged. Downstream from the hydraulic jump the flow is, of course, tranquil.

Standing waves may be classified in three distinct types, examples of which will be readily found in all salmon and trout streams.

(*a*) *The Undular Wave* (Fig. 5A) occurs frequently near the heads of pools where the inflow is of relatively low kineticity. With slight fluctuations in the velocity of the inflow around the critical velocity, $\sqrt{gh}$, these waves vary considerably. They are not likely to present any obstacle to migrating fish as the ratio of kinetic to potential energies in the inflow is low.

(*b*) *The Free Standing Wave* (Fig. 5B). With rising water levels upstream or in pools with a steep inflow, kineticity rises and the forward wave of undular type increases in size with the gradual disappearance of the secondary waves. The crest of the wave now breaks and an aerated vortex or roller is formed on the upstream side. The ratio of kinetic to potential energy in the section ahead of the wave is now high, the wave presents a generally disorderly appearance and, according to Bakhmeteff and Matzke (1936) is subject to 'violent and apparently inordinate oscillations. Thus the position of the toe of the jump varies continuously, up stream and downstream. Even greater agitation is noticeable in the roller, to which at first, one may be led to doubt whether any uniform or stable laws apply.' In an earlier paper (Stuart, 1957) it was noted that, during spawning runs of trout, all activities of movement and spawning were halted under these conditions, the standing waves, formed in the pools as the result of increasing discharge during a spate, acting as barriers.

(*c*) *The Submerged Wave* (Fig. 5C, D). Where the inflow is from a steep weir or a waterfall and the level of the pool rises further owing to flooding or damming, the standing wave will approach the toe of the weir or the foot of the fall and be driven under by the 'live vein' of falling water. Smetana (1935) found that in a submerged wave there was less air mixed up with the water. It is under these conditions that migratory salmonids hurl themselves most frequently and persistently at broad, virtually impassable weirs, but, as will be shown below, the identical conditions are of undoubted assistance at vertical waterfalls.

The stimulatory effect of change of rate of flow on salmonids was described by Elson (1939) for *Salvelinus fontinalis* where a sudden increase in current strength and amount of turbulence resulted in increased activity with movement upstream. The reaction has also been used to induce salmon to run upstream under the influence of artificial spates (Hayes, 1953). In the present case it is important to distinguish between stimuli that initiate migratory movements and the factors dealt with in the experiments under review which are concerned with halting, delaying and restarting such movements which may have commenced weeks and even months earlier.

In the last experiment it was clear that the relatively heavy flow of water was the origin of the stimulus that resulted in leaping activity. The earlier experiments demonstrated that the chief stimulus for the observed behaviour was likewise an enhanced flow while the other variable factor examined, the pool depth, in relation to flow, had little effect other than to assist, or hinder, the task of the fish.

When the depth of the pool was slowly increased, the standing wave moved closer until it became submerged at the foot of the weir. The pool depth was now 5 inches and the height from surface of the pool to crest of weir, $4\frac{1}{2}$ inches. Entrained air bubbles became greatly reduced in number but sufficient remained in the current to enable the course to be defined. It was thus seen that the jet of water struck almost vertically downwards, while an upward jet arose alongside with sufficient velocity to raise a clearly defined hump on the surface of the pool, close in front of the falling water. From the crest of this hump the fish leapt singly and in twos and threes in rapid succession to clear the obstacle and vacate the lower pool (Fig. 4F). Fresh groups of fish were introduced from time to time and they behaved exactly as the first group.

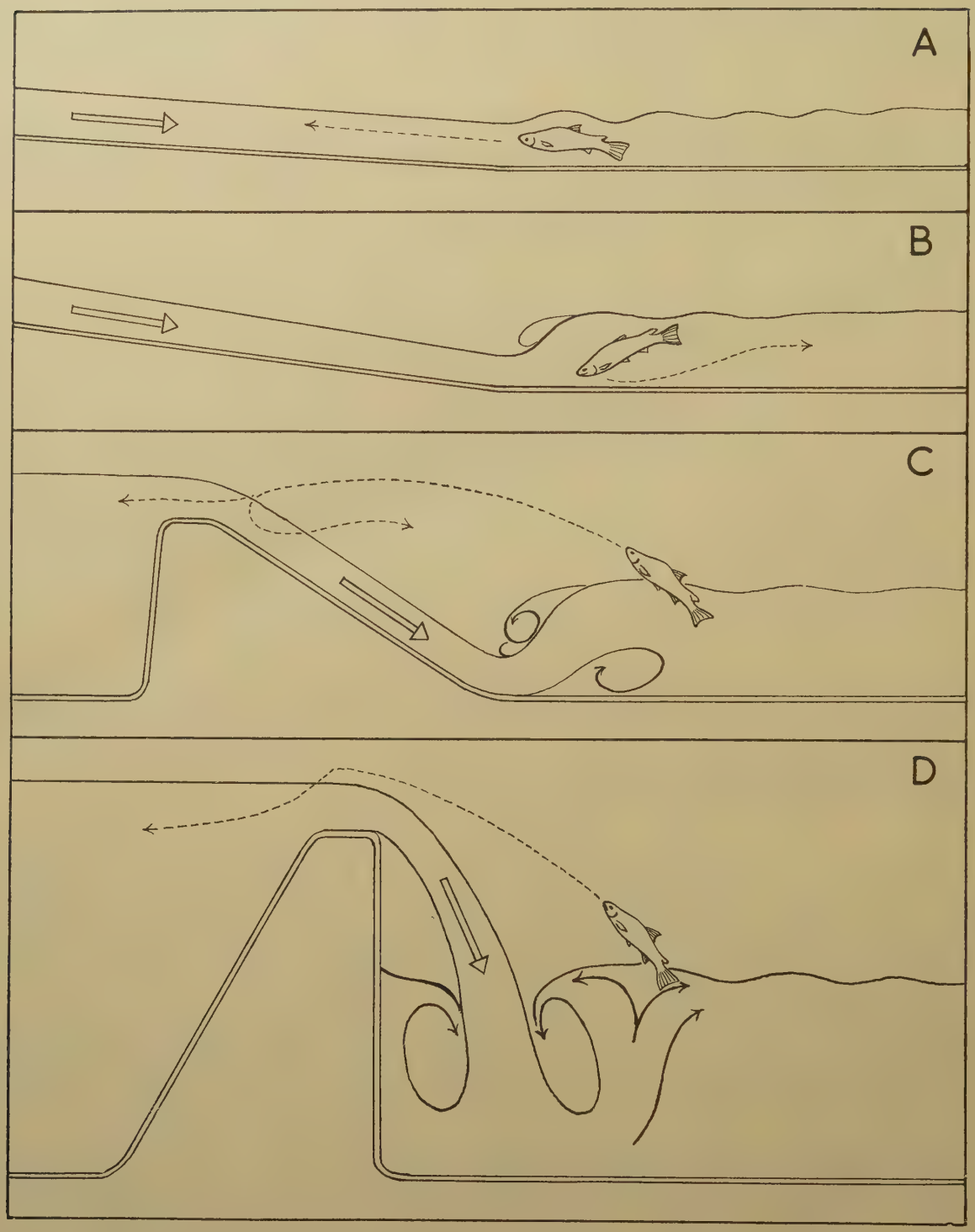

Fig. 5 The reactions of salmon and trout to standing waves. Explanation in text.

Chiefly in order to concentrate this activity in a smaller field but also to simulate more closely the normal layout of a fish ladder pool, a weir with a 5 inch spillway was substituted for the broad crested weir used hitherto. The impact on the pool was thus increased, then further increased by passing the maximum rate of 30 gals/min. through the channel, without altering the accuracy of the leaps, although the 'target' had now contracted by two thirds. Further tests on the precision of the leaps were made and these will be discussed below.

The level of the pool was now raised until the type of flow illustrated in Fig. 4G was obtained. Instead of striking almost vertically downwards, the 'live vein' of the inflow passed down the pool close to the surface in a series of undulations which fluctuated violently, forming temporary standing waves about fourteen inches from the weir which showed no discernable periodicity. The behaviour of the fish in the pool was likewise erratic. Some attempted a leap from a distance: many, however, tried to swim over the weir but, finding the velocity too high when they approached closely, were eventually displaced to the side or below the vein. It was observed that the initial definite approach commenced as much as sixteen inches from the weir with the fish swimming vigorously and making increasing efforts to cope with accelerating velocity. Ultimately, when maximum effort produced no progression, the fish turned out of the current. Exactly similar behaviour was observed when a weir with a submerged orifice was substituted for one over which fish were leaping successfully (Fig. 4H). The path of the fish in this case was near the base of the pool in line with the high velocity jet. With the submerged orifice some success was obtained in passing fish through when the discharge was reduced, but great difficulty was experienced in balancing the levels of the pools. It became very clear, however, that the amount of energy that would be expended by a fish in passing a succession of such orifices must be many times greater than that required to leap over an equivalent series of more natural obstacles.

It was of special interest to note that the greater the velocity of the underwater jet the more the fish were attracted, but when the velocity was reduced to a rate that permitted progression through the orifices its attractiveness was also reduced.

Over a period of several days the rate of flow was reduced and increased within the range of 8 to 30 gals/min. and the pool depth around 5 inches. The experiment was interrupted for occasional periods of about 24 hours during which the flow through the channel was negligible. Any effect of the resting periods, however, could not be determined as the experiments took place at the height of the migration season and the response of the fish was 100%. Activity, nevertheless, was much greater at the higher discharges and this was most readily measured by the incidence of 'group' jumping, i.e. when two or more fish leapt at the fall simultaneously. The following observations were made mainly with discharges around 24 gals/min. which gave good conditions of visibility.

While leaping was in progress all fish in the pool were congregated near the fall swimming slowly and 'purposefully' with head pointed downward at an angle of 20° to 30°, in midwater or near the surface. The amplitude of body and tail flexions was large compared to normal movements in a current and here, apart from the evidence of entrained bubbles, the influence of a strong current was shown by the low and often negative rate of progression. Fish approaching the fall from the sides were swept back, or at times found their way to the weir face behind the fall where they remained for a few seconds only, vertically—head down, tail up. Of particular interest were the reactions of the fish that met the upward current in front of the nappe. No evidence of any avoiding reaction could be seen as the fish rose with the current to break the surface, usually head first, but frequently the whole back was exposed. All that could be distinguished was the eruption at the surface as the fish left the water and sped through the air, body truly aligned to its direction, to strike the crest of the nappe and disappear under the surface of the upper pool. High-speed photography showed that in most instances as the fish left the surface it was surrounded by a cylindrical sheath of water from which it parted near the crest (Plate 1). Not every fish leapt at first emergence however, but, with the almost perfect conditions of the experimental arrangements, this was the general rule, and failures were few.

The uniformity of the results and the fact that the fish, without exception, all leapt from the same small area on the 'hump' created by the strong upward current pointed strongly to the importance of this unquestionable aid.

'Artificial Fish' Experiments

To test the effect on an inanimate body incapable of choosing its path or, in other words, responding to directive stimuli, a celluloid table-tennis ball was pierced, filled with water and then allowed to fall over the weir. Entrained in the current, it passed below the surface of the pool and continued downwards. About an inch from the bottom its descent was arrested and it remained in the axis of the underwater jet bobbing vigorously, but completely captive (Plate 2). For long periods it continued in this position, but eventually, owing to the minor fluctuations in the velocity of the jet, it escaped, rose rapidly to the surface in the adjacent upward current, moved 'upstream' into the nappe and repeated the sequence. The forward movement into the nappe from the apex of the 'hump' suggested another test for the dye and accordingly, when a crystal, held by fine forceps, was applied to the apex it was seen that a positive current from this point led into the front of the nappe. A tentative suggestion as to the origin of this current is that it may be part of an attenuated roller in front of the standing wave that became submerged in the deepening pool.

The water-filled ball was now replaced by another ball weighted with lead shot until it just floated under the surface and the procedure was repeated. No significant difference was apparent in the behaviour of this ball until it escaped from the downward jet. Then, like the first ball, it shot to the surface, but owing to its greater buoyancy it broke through the surface film of the water and was then *projected* '*upstream*' to strike the nappe. Occasionally, but chiefly at the maximum discharge when turbulence in the nappe became evident, it broke away to drift down the pool. In later experiments, in a pool designed to the proportions of a natural fall pool, the ball could be left to perform numerous circuits unattended for periods of up to 24 hours at least.

The leaps of the ball upstream, so closely paralleled by the leaping fish, demanded further investigation. As it was considered possible that a rotatory movement imparted by the current might have been responsible for the directional element in the leap of the ball a model 'fish' was designed to test this. A similar celluloid ball was used and to one pole a wedge-shaped 'fishtail' equal in length to the diameter of the ball, was attached rigidly. Lead shot was introduced as before but was fixed with melted paraffin wax slightly below the opposite pole. 'Dorsal' and 'ventral' aspects were distinguished by painting one side. The finished model resembled quite closely an inflated *Tetrodon* and when placed in the pool floated just under the surface with the tail tilted slightly upwards.

The model behaved exactly as before and maintained its fish-like orientation throughout the circuit, giving no indication of any forces at work beyond the uplift of the current and its own partial buoyancy. It was also found possible to have both tailed and tail-less models captive together in the downward jet.*

The results of these experiments show that, confronted with an obstacle such as a waterfall, the fish await certain conditions of discharge (see also p. 28) and do not usually attempt to leap until these are present. Observations in the field confirm that these conditions arrive with rising water levels in the river and that then the fish will leap, even at an unsurmountable obstacle.

The stimulus for leaping therefore must be associated with physical phenomena related to these conditions and it has been shown in the experimental channel that leaping was initiated when the ratio of kinetic and potential energies was high in the section of water just ahead of the fish. That is, when conditions were such that a standing wave was formed. It appears, therefore, that the fish attempts to leap over a high energy front instead of forcing a passage, by swimming, through the 'barrier', even when a solid obstacle is absent.

*In another experiment a vertical hosepipe of 1 inch bore delivered the water supply under pressure into a surge chamber at the head of the channel measuring $2 \times 1{\cdot}25 \times 1{\cdot}5$ feet. Celluloid balls filled with water or suitably weighted with lead shot were placed in the chamber and the maximum supply turned on.

Within a few seconds one of the balls was trapped in the jet and by raising or lowering the hosepipe the ball could be held captive and almost motionless about an inch from the base (Plate 3). In this position a single ball could be left indefinitely. In company with other balls however, as each in turn was trapped by the jet it displaced the other, and so on.

When the hosepipe was slowly raised, the ball followed slightly more slowly, developing at the same time a lateral oscillation that increased in amplitude with distance from the base and the orifice of the pipe. Eventually the amplitude so increased that the ball was swung clear of the jet. Conversely, when the hosepipe was lowered, the ball immediately began to oscillate vertically and when it ultimately touched the base it rebounded clear of the jet and could not be trapped again. At the point where the ball remained captive and relatively motionless there was obviously a balance of energies between the force of the jet at that point and the 'rebound' from the base.

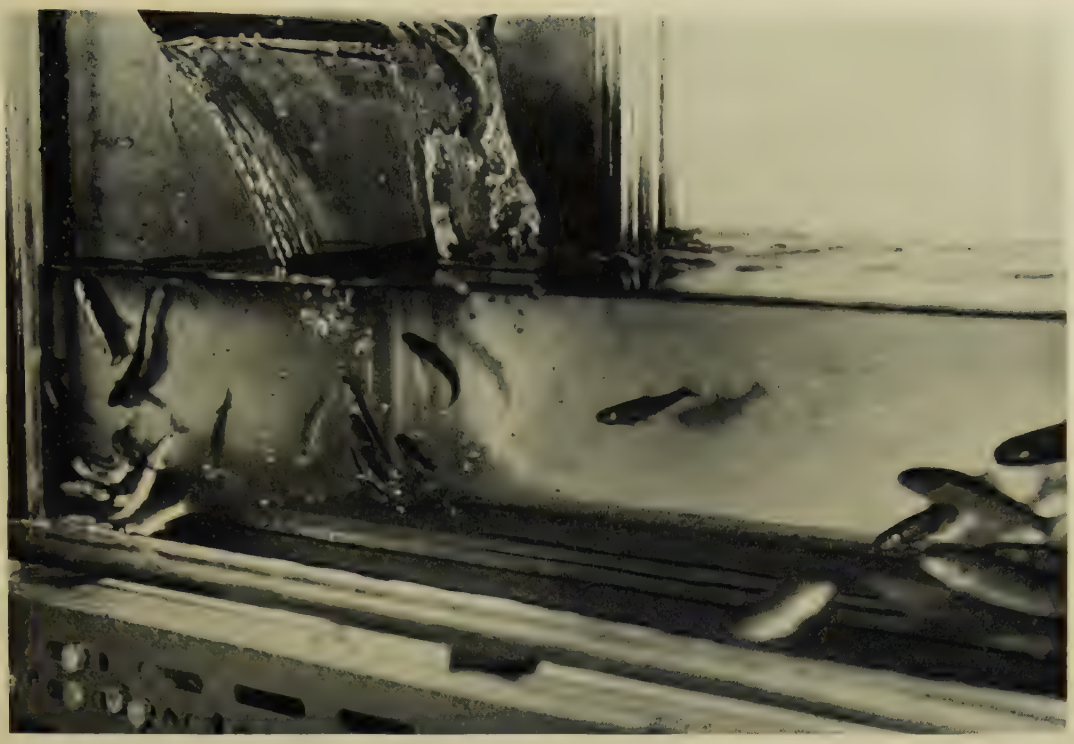

Plate 1 Leaping salmon parr showing cylindrical water sheath.

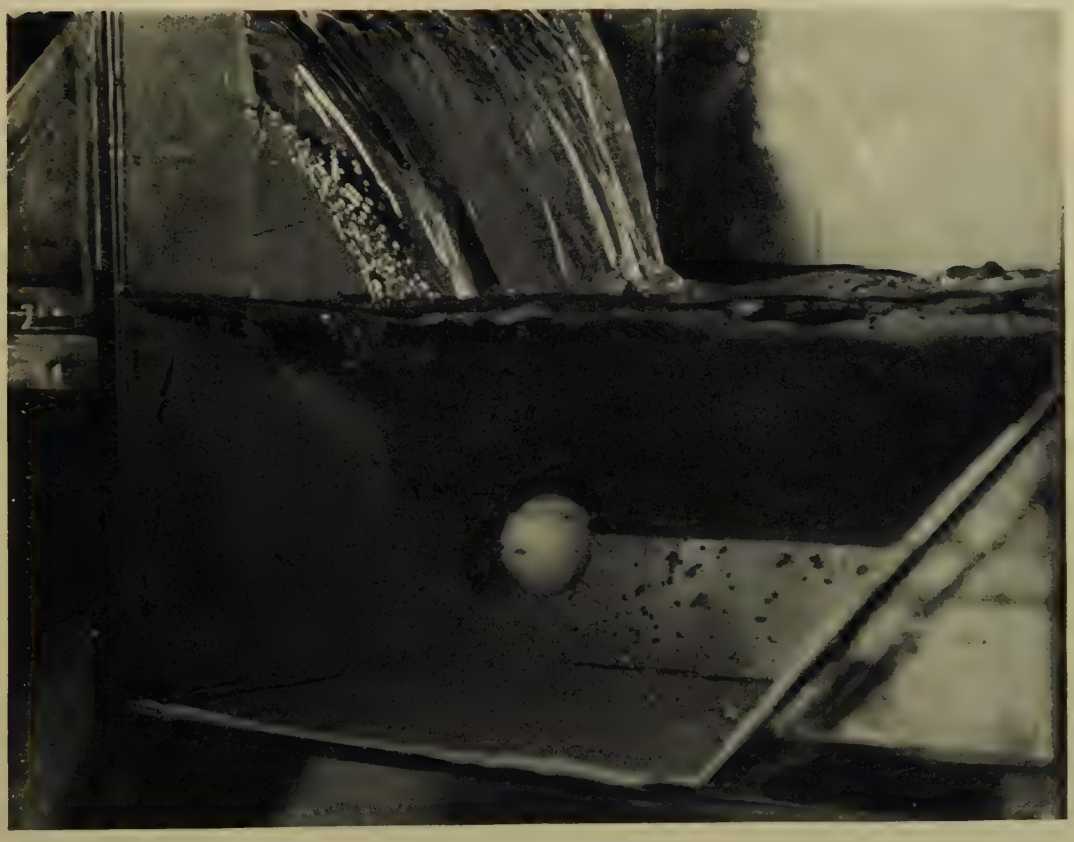

Plate 2 Semi-bouyant celluloid ball held captive by hydraulic forces beneath the surface of the pool.

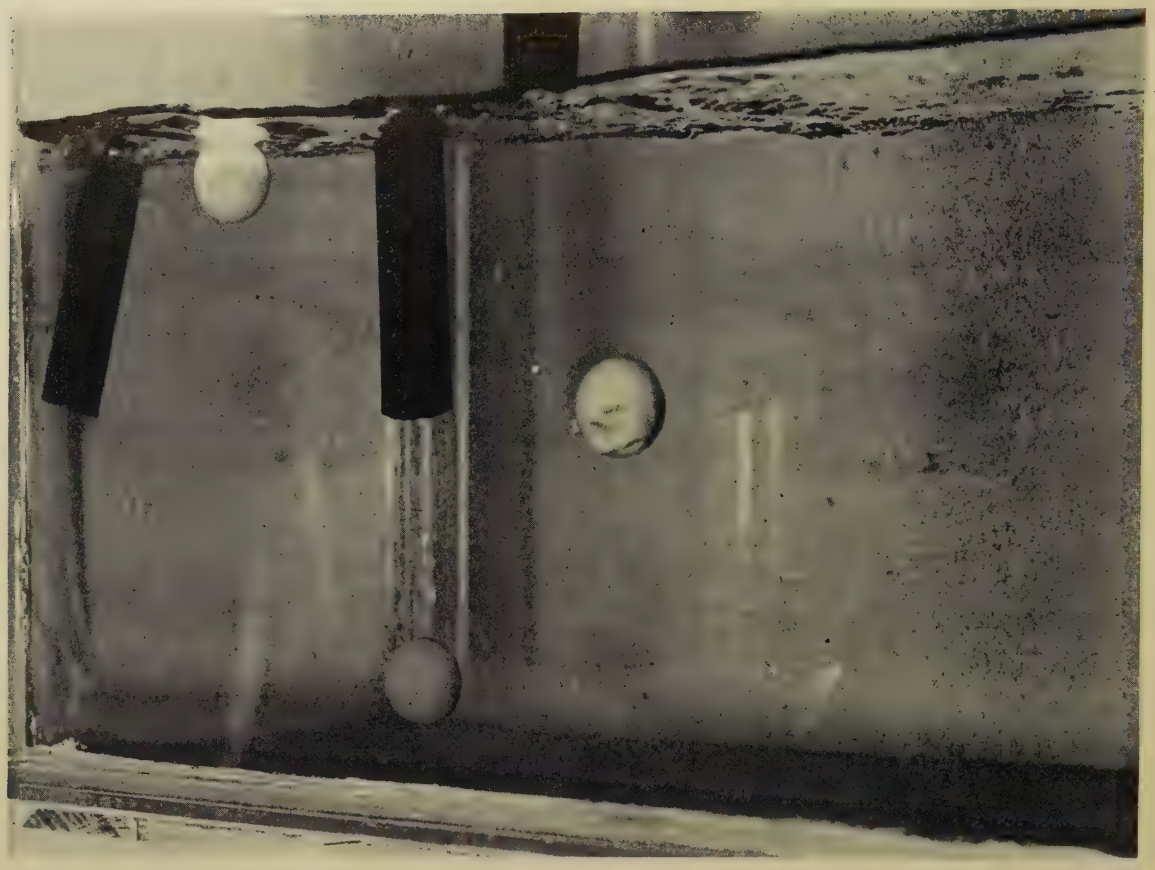

Plate 3 Water-filled celluloid ball held captive in jet from hose-pipe. Two similar balls circulating in the local turbulent currents.

Plate 4 Passive entrainment at the 'toe' of the fall. Explanation in the text.

It has been shown that when, with increasing depth in the pool, the standing wave became submerged, leaping continued and, confronted with a vertical barrier, the fish were able to surmount it, the leap exhibiting at the same time a certain accuracy of height and direction. The experiment also showed that, with increasing kinetic energy in the falling water, the consequent more successful leaping activity could be related to the presence of a strong upward current which was associated with, and probably directly proportional to, the downward current.

The behaviour of the celluloid balls, however, demonstrated the importance of the depth of the pool. If the pool was too shallow the force of the downward jet caused the current to splay outwards along the base; if too deep, the force was dissipated some distance from the base. It was therefore important to determine the relationship of height of fall to depth of pool for maximal upward current, and the experiment was now transferred to the 'ladder' pools.

The Formation and Natural Dimensions of Fall Pools

Here it may be stated that the design of these pools was based on measurements taken from a natural fall pool and a relationship was derived that gave the depth equal to 1·25 times the height of fall. Accordingly it was gratifying and instructive to find the balls held captive in the specially designed pool about one inch from the base, as in the surge chamber, and to note an improved leaping performance.

Examination of natural fall pools reveals a certain uniformity which is particularly evident at waterfalls known to be easily passable by migratory salmonids. Such falls as are known to be impassable or difficult are not necessarily so because of their height, though excessive height is an obvious limitation. It is quite possible, however, to find that salmon can leap up a twelve foot fall and yet be barred by

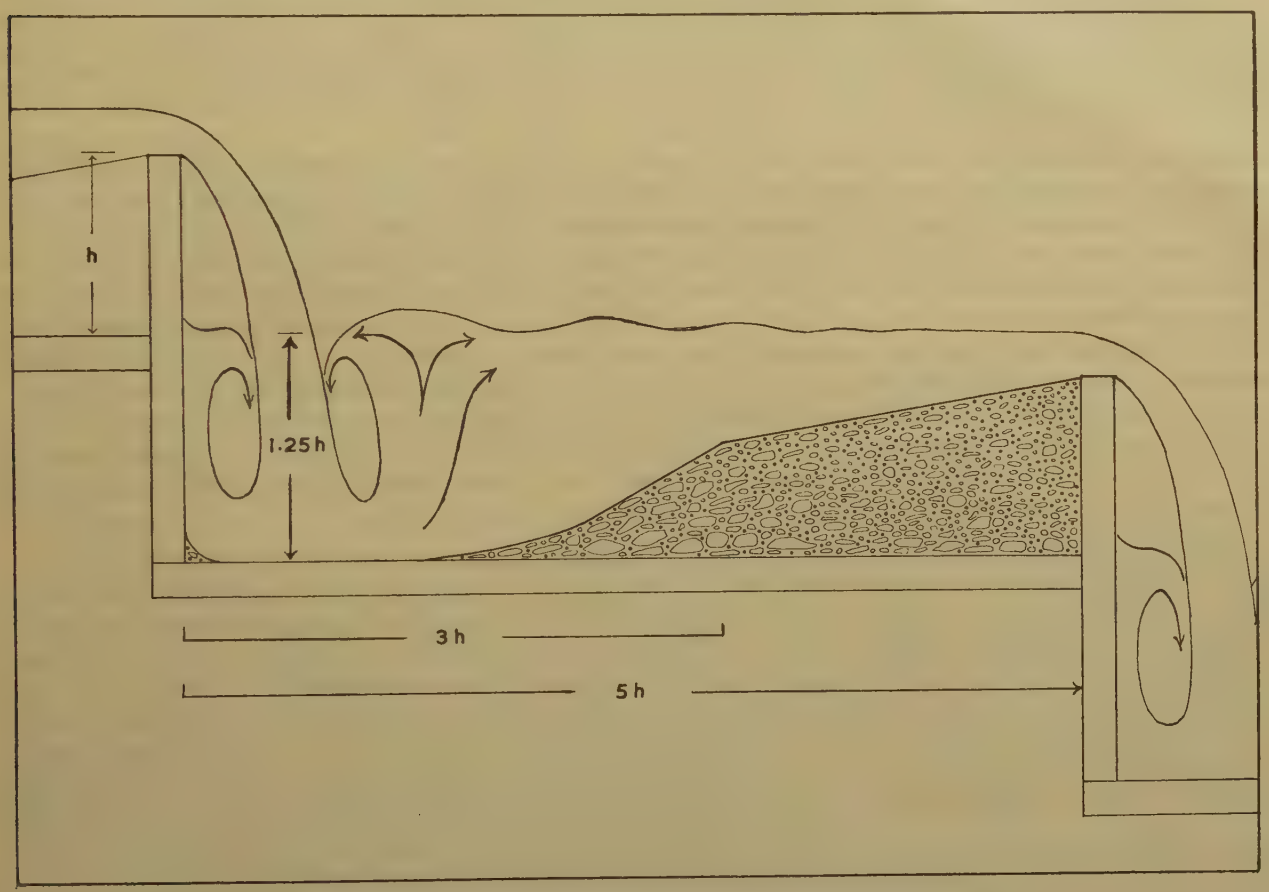

Fig. 6 Section through ladder pool. Explanation in text.

a fall (or weir) half that height, or even less, and the explanation obviously must reside in some characteristic other than height alone. It is thus found that most passable falls are characterised by a pool of much greater diameter than the breadth of nappe of the falling water and in general, the depth of the pool is directly proportional to the height of the fall. At the tail of the pool the stones and gravels have a steeper angle of rest than is found in the normal pool of easier gradient, and this may be as much as 45° compared to from 5° to 10°. If the water drops vertically into the pool the face of the fall is undercut, but if the fall is relatively low and the velocity retains a horizontal component the undercutting is reduced. These characteristics will be discussed further when dealing with the field work; they are mentioned here because it was found possible to reproduce them in the artificial fall pool by allowing the water to carve its own bed.

The ladder pools were filled to the crests of their weirs with a mixture of gravel and sand, 50% of which comprised stones from $\frac{1}{2}$ inch to $1\frac{1}{2}$ inches in diameter. Water passing over the weirs displaced much of this material rapidly as the discharge was increased and at maximum discharge the scour holes were well defined in all three pools (Fig. 6). The force of the upward current was clearly demonstrated while scour proceeded as stones over $\frac{1}{2}$ inch in diameter were raised to the surface of the pool and often held in suspension, while smaller materials were swept away into the lower pool.

Relative rate of scour is a function of the ratio of jet velocity, to settling (or sinking) velocity of the granular components of the river bed. If the components are non-uniform, the scour hole becomes paved with coarser material, the smaller particles being carried away, thus increasing the effective settling velocity, which results in a reduction of rate of scour (Leliavsky, 1955b). In this manner the waterfall regulates the depth of its pool, and in the experimental pools the chosen depth was shown to be very close to the requirements of the discharge, for only a circular area of the base about $1\frac{1}{2}$ inches in diameter was exposed by the scouring action while the remainder of the gravel was disposed uniformly around (Fig. 6). When large amounts of the gravel mixture were now introduced above the ladder these swept down through the pools, but left the scour holes unaltered, thus demonstrating the close relationship between discharge and depth of pool.

The dimensions of the ladder pools therefore met the requirements as exemplified by the natural fall pool, but it was observed that the crest of the nappes of the middle and lower pools were not so smooth as that of the upper pool and that more air was entrained. As originally designed, the length of pool was made equal to four times the height of the weir to comply roughly with the measurements of the natural fall pool taken from the fall to the apex of the 45° bank at the end of the pool. It was found however, that downstream from this point the upward slope of the gravel became abruptly less and was, in fact, identical with the slope at the tail of a normal pool, i.e. about 5° to 10°. When this slope was reproduced by increasing the length of the ladder pool there was a marked diminution in turbulence at the next weir crest, together with a decrease in aeration. The minimum recommended length therefore is five times the height of the weir as in Fig. 6. In addition to the smoothing effect on turbulence, the provision of this gentler slope in fish ladders is of some importance when the ladder is utilised by downstream migrants, and this will be discussed later (p. 37).

Throughout these experiments weirs with spillways of various types and widths were used (Fig. 2), each of which affected in its own fashion the characteristics of the nappe. The broad spillway extending from side to side of the channel gave the smoothest overfall but required the greatest discharge to attract the fish and was therefore uneconomical of water (Fig. 2A). The width of rectangular notches however, could be adjusted to match the available discharge and these proved satisfactory in operation (Fig. 2B). Triangular notches, on the other hand, unless very narrow, required heavier discharges for comparable effects and entrained more air (Fig. 2C). Trapezoidal notches (which may be considered as triangular superimposed on rectangular) were the most satisfactory of all, giving a relatively smooth crested nappe which converged slightly before striking the pool below, thus increasing the power of the downward current (Fig. 2D). In the model ladder, the width of spillway used most frequently, was equal to half the width of the channel. In a prototype designed for salmon a notch width of at least two feet may be considered to be a safe minimum. The optimum breadth of channel as shown by the disposition of the

gravels scoured in the ladder pool (Fig. 6) showed that, for the spillway used, this was equal to three times the height of the weir. In a prototype however, this would require to be considered in relation to all other parameters of which the available discharge would be the decisive one.

The Orientated Leap

During numerous observations of fish leaping at weirs of assorted heights and widths, which were often surmounted in sequence as the fish progressed from pool to pool, the accuracy of the leaps was marked. Under the more or less favourable conditions noted above, the fish leapt from the 'hump' and almost invariably touched water again exactly on the crest of the nappe where a few strokes of the tail placed the fish in the pool above. Although successive weirs differed in height and breadth, no fish was observed to miss the aperture or to leap more than one inch higher than the crest. The rare attempts that did not attain the height of the crest were most probably due to failures of coordination, for even in the geometrically uniform channel pulsations in the currents were evident. A simple Pitot tube placed on the hump caused by the upward current and using the normal pressure head as the velocity head, showed large fluctuations. Such misleaps were much more common in natural rivers and were related to irregularities of flow or multiple and converging waterfalls, but even here when one of a choice of routes attracted more and more fish, failures of this kind became rare.

This remarkable accuracy was doubtless partly due to the location of the 'hump' in relation to the aperture of the spillway which ensured that the fish leapt in the direction of flow from a central position. This did not account for what appeared to be a very precise estimate of the height on the part of the fish, though at first it was considered possible that the fish might have derived some information from the relative strength and direction of the upward current and this cannot yet be discounted. However, a chance observation provided a clue which, on further investigation, gave a plausible explanation. In order to prevent fish from entering a pool where another group was under observation, the lower weir was fenced off by placing a grid of heavy gauge square meshed wire closely against the upstream face of the weir. It was found however, that unless this grid extended to the cover over the channel, fish leapt over it, although the water was falling through the grid and over the weir at the normal level. Further observation showed that while the majority still leapt at the crest of the nappe, about 25% leaped directly at a two inch gap between the top of the grid and the cover and passed through cleanly. Experiments were then conducted with grids of various heights and similar results were obtained with the fish leaping just sufficiently high to clear the grid. It was now apparent that the fish were 'aware of an obstruction' and could adjust the leap accordingly. As it seemed most likely that the reaction was to a visual stimulus and therefore related to a contrast of light and shade, the grid was inspected from approximately the position of the fish in the pool below when it was seen that its effect was to reduce the contrast between the crest of the nappe and the background. When the grid was now covered above the water level with an opaque black fabric the proportion of leaps over the grid increased to about 40%. It was during this experiment that the only recorded instance of a fish trying an alternative leap after an initial failure (due to the presence of the fence) was obtained and it is considered that this was owing to the unusual nature of the experimental conditions.

Visual examination of the crest of a weir or waterfall from a standpoint downstream lends confidence to the theory that the fish may aim at a sharp boundary between light and shade. The predominant tone on the crest of a smooth weir is a dark band, superimposed on which is a narrow line of reflected light. Immediately below the dark band the more or less striated nappe is neutral in tone but may become brilliant in sunshine (Fig. 2; Plate 7). Against a bright sky background the dark band is sharply contrasted; against a darker background, e.g. trees, rocks, dark clouds, the narrow line of reflected light maintains the contrast. The continuity of contrast at the boundary between water and background is therefore, under normal conditions of daylight, always likely to be clearly visible. In the laboratory, no fish was observed to leap when a dark cover was placed over the channel, and in the field all leaping ceased abruptly at dusk and under heavily overcast conditions.

A later observation, made under most unusual conditions, appears to lend further support to this theory. At the beginning of all these experiments, when the water in the channel was slowly brought to

movement from a static condition, no reaction whatsoever was obtained from the fish until a certain definite overfall was apparent at the weirs (p. 8). However, during the course of a further series of experiments in which the fish had been leaping vigorously over the various obstacles, the water supply was turned off and the levels of the upper and lower pools eventually coincided. It was of considerable interest to note that the fish in the downstream pool still continued to leap at the dewatered weir to clear it with comparable accuracy and complete their trajectories into the upstream pool now five to six inches below the crest of the weir. Still more unexpected was the behaviour of the same fish which, after an interval occasionally as brief as 30 seconds, repeated the performance in the opposite direction. (Particular care was taken to keep the observer hidden from the view of the fish as a matter of routine, but it was characteristic of all the reactions observed during this investigation that the fish appeared to be relatively insensitive to the presence of observers even when no precautions were being taken.) Checks were made with the use of dye but no currents were observed on either side of the weir. This behaviour was clearly a 'hangover' from immediately previous activity and it ceased after about 15 minutes of static water conditions. It could not be re-induced until the whole cycle of events was repeated.

Thus in the absence of any coincident stimulus or directive from falling water the fish were sufficiently aware of the obstruction to reorientate their leaps correctly to the crest of the weir.

Initiation of the Leap

As mentioned above, all leaps commenced from, or very near, the surface of the pool and it was not possible, by interpreting specific directional movements, to tell when a fish was about to leap. Many approaches were made which merely resulted in the fish being raised bodily to break the surface, then retire. The leap, when it did take place, was indicated by a quick body and tail flexion which may perhaps be best described as a 'flip' of large amplitude. Generally this movement was partly obscured by the sheath of water which rose with the fish (Plate 1) but the amplitude of the flexion was so large that

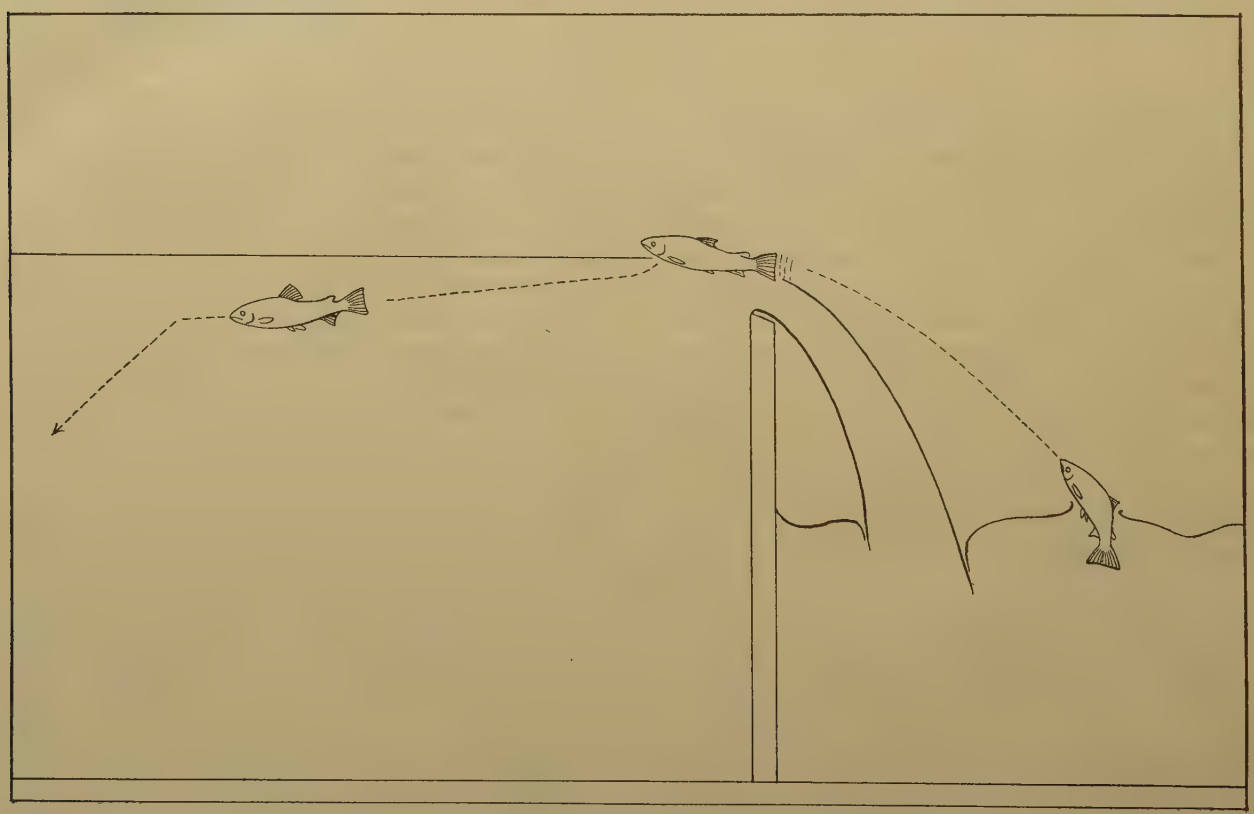

Fig. 7 The re-entry and subsequent reorientation after the leap.

it is not difficult to understand how early writers were convinced that the fish 'took its tail in its mouth'. Judging by the symmetry of the water sheath, it would appear likely that this flexion followed rapidly on at least one other.

As it rose out of the pool, the fish travelled through the air clear of the nappe, its body aligned to the crest of the weir, rigidly and without sinusoidal movement, but with the tail vibrating. There is possibly an analogy here with the racing of a ship's screw as it leaves the water momentarily in the trough of a wave.* On the fish re-entering the water at the crest of the weir the frequency of vibration decreased rapidly with increasing amplitude and the fish was propelled upstream into the pool above. Above the weir, the initial impetus carried the fish forward, descending at a shallow angle of 8° to 10° from the surface for a distance of about 12 inches, at which point it invariably checked its progress. After a momentary hesitation it swam directly to the bottom at an angle of approximately 45° (Fig. 7).

At natural waterfalls, where at times far from ideal conditions obtain, many abortive leaps may result, but generally it will be found that when, under the continually changing values of discharge etc., favourable factors eventually coincide, successful leaping reaches a peak and leaping may, indeed, only then be evident. Under ideal conditions as outlined above, no fish entered the water at the crest of a weir or fall headfirst, but always the first part of the body to touch the water was in the ventral region of the pectoral fins. The body of the fish then sank below the crest with the tail still vibrating and acting immediately on contact with the water to propel the fish forward into deeper water. This reaction will be referred to again (p. 26) when dealing with a 'difficult' natural waterfall where no fish could reach the pool above without the immediate production of a short burst of swimming at the end of the leap.

Territorial Behaviour

Throughout these experiments no trouble was experienced from the normal aggressive behaviour of the salmonids. Except in more or less static water conditions no hierarchical distribution of the fish was apparent below the weirs such as had been noted elsewhere in the laboratory (Brown, 1946) and in the field (Stuart, 1953b). In the present study it was observed that the tendency of the larger fish to dominate the smaller became reduced and ultimately disappeared as the numbers held in a pool increased. This agrees with earlier observations (Stuart, 1953b; Munro and Balmain, 1956) when it was noted that, on the approach of spawning time, adult trout congregated in shoals in lochs and reservoirs near the mouths of the spawning streams, thus reversing their normal behaviour during the rest of the year when they are distributed over the whole of the loch. Marked aggressive behaviour, however, is immediately resumed when the fish attain the spawning beds (Stuart, 1953b) and individual fish will not tolerate the near presence of another, unless of opposite sex.

In the present work it was of interest to note comparable territorial behaviour in immature fish during the performance of a migration similar in most respects to that of mature fish, except for the ultimate spawning behaviour. As already mentioned, before leaping commenced, relatively large numbers of fish peaceably occupied the lower pool. Eventually one fish leapt and entered the upper pool and was soon followed by another. The immediate reaction of both fish in the upper pool was the performance of an intimidating display with each fish circling the other alternately and lunging with mouth wide open. Succeeding fish behaved in the same manner and were also attacked by the earlier entrants. Similar behaviour continued until, with increasing numbers in the upper pool, it appeared to be difficult for any fish to select an antagonist. Thereafter all fish swam about together, apparently indifferent to each other's presence. This behaviour was found to be invariable and all fish responded irrespective of size.

Tests were made with an upper pool reduced to 3 feet in length and it was found that aggressive behaviour ceased when about 10 fish occupied the restricted area. On several occasions two fish leapt simultaneously to enter the upper pool and on each occasion their immediate reactions were aggressive. There can be little doubt of the value to a species of this temporary blocking of an aggressive instinct at

*Since writing the above the same analogy was found in the following descriptive account by Denil (1938) of leaps by fish for the purpose of the capture of insects in flight:

"Ces bonds, . . . attendraient plus de 50 cm. de hauteur et maintiendraient le poisson hors de l'eau assez longtemps pour que l'oreille puisse percevoir la grêle musique que produit le frétillement du corps du poisson. Car celui-ci, au cours de son séjour aérien, paraît animé d'un mouvement vibratoire qui n'est, peut-on penser, que le prolongement de son action locomotrice habituelle marchant à un rythme accéléré par l'emersion, comme le mouvement d'une hélice qui émerge et s'affole."

times when individuals are necessarily crowded together in a mass migration. No evidence, however, was obtained that individuals from an aggregation leapt more readily than fish held in isolation, but later in July (when the urge to move upstream was abating) the introduction of a very much larger brook trout (*Salvelinus fontinalis*) prevented many leaps owing to its pugnacity. It may be of interest to record here that two brook trout performed the leaps as competently as the other salmonids.

FIELD EXPERIMENTS AND OBSERVATIONS

The chief field observations in relation to the present study were made at the falls of the Pot of Gartness on the River Endrick during 1959 when, owing to the long dry period of the summer months, large numbers of salmon, sea trout and brown trout had accumulated below these difficult falls to await the advent of adequate rainfall. This did not arrive until the middle of October, but with minor rises in water level during the preceding months a few sea trout and brown trout had penetrated to some of the upper tributaries. With the first rains of October which, however, had little effect on the main river, the smaller obstacles in the tributaries became passable. The opportunity was then taken to make some *ad hoc* experiments in the channel of the Rednock Burn where the natural features of the stream permitted simple alterations to be made. This little stream provides good spawning ground for sea trout and brown trout in its upper reaches and, at the site chosen for the experiments, the stream varied in width around 2 and 3 feet, with numerous rapids, falls and pools. Within recent years the stream at this place had made a diversion from an older channel and its new bed was now stable except for one small section where it encountered a bed of clay, into which it is still slowly cutting back. At this point owing to the erosion, a vertical fall about 24 inches high and of equal breadth was formed in the clay and the stream had scoured a hole beneath which formed a pool in the soft substratum of about the same depth. The contours of the pool were otherwise approximately similar in proportion to those formed artificially in the laboratory pools (p. 18).

On arrival at this pool while a small run was in progress, sea trout and brown trout, measuring from 15 cm. to 30 cm., were entering the pool at frequent intervals, and, without apparent hesitation, passing over the miniature waterfall. At the same time salmon parr were leaping at the 24 inch obstacle and surmounting it with only an occasional failure. The parr were of a very uniform length of about 12 cm. As a result of a slight irregularity at the top of the vertical bank of clay the greater part of the water fell into the pool near the right bank and all fish were leaping from this side. When the water was diverted towards the left bank by placing a large stone on the right side at the top of the fall, leaping, when it recommenced, was directed towards the left. Similar manipulations with stones at each side directed the fish to the centre of the fall and through a gap between the stones of only seven inches. In almost every case, owing to the uniformity of the hydraulic conditions, the fish leapt accurately to the lip of the fall and proceeded upstream in one movement.

The scour hole was then filled with turves which were covered by a flat stone and the depth of the pool was thus reduced to about 6 inches. Over a period of thirty minutes the pool was kept under close observation and trout were seen to enter but none attempted to leap. When the pool was restored to its original state leaping was resumed about ten minutes later.

The stream was also partially diverted into its old channel and leaping was stopped and restarted at will over a similar period by opening and closing the diversion. Salmon parr endeavoured to swim up the vertical face of clay when the nappe was adherent but often made a diagonal leap across the face from the right side where the volume of water was greatest. This type of leaping however, was considered to have resulted from a vigorous but deflected swimming effort which had a partial success owing to the diagonal course taking the fish progressively into much lower velocities.

At a later visit, with the streams nearly bank-full, runs were again in progress. The frequency of the leaps over the clay bank fall was about the same as before, but no parr were leaping. A discarded and rusty sheet of iron roofing conveniently to hand was wedged against the fall to form a chute about six feet long with a slope of roughly 20°. This resulted in considerable scouring of the tail of the pool and cessation of all leaping. Within a few minutes the scour extended the pool downstream and the action of

the water was assisted by removing by hand several large stones which were used to block the sides of the chute. No standing wave was formed owing to the steep gradient below the pool. After an absence of about two hours the site was revisited. It was then found that sea trout and brown trout had accumulated in several pools below the fall and also in the fall pool. Pairs of fish were present in some pools above the fall but there was no aggregation there. During the interval, however, the water level had fallen two inches and salmon parr were trying to swim up the chute on the left side where the velocity was lowest but, chiefly owing to the length of the slope, without success. A further period of thirty minutes produced one attempt by a larger fish, which also failed. The stream was then restored to its natural conditions.

In isolation these very rough experiments are by no means conclusive. In the last experiment some fish may have negotiated the chute successfully during the observer's absence or some other factor may have retarded the activity, although no aggregations of fish below the fall were found during the earlier experiments when the water level was very much lower. But in general they confirmed many previous observations and some experiments in the laboratory and are not in conflict with the observations to be described presently at the Pot of Gartness.

According to Calderwood (1909), 'The two obstructions at Gartness are, in descending order, first the double obstacle of the dam-dyke and fall at the village of Gartness; and second, beyond an extensive loop of the river course, a more serious fall at the Pot of Gartness. That salmon manage to surmount both obstacles is sufficiently evident for I have seen numbers of fish above; but certainly the ascent must be accomplished with difficulty.'

As already mentioned, being now fallen into disrepair, the dam-dyke is no longer an obstacle except in very low water when fish are unlikely to be on the move; and the lesser falls associated with the dyke are little more than 'rapids'. These falls will therefore not be considered here.

The lower falls however, which debouch into the deep pool known as the 'Pot' are, apart from their scenic qualities, a well-known local attraction when salmon and trout are leaping. At certain times large numbers of fish may be seen in the air simultaneously, yet, although the falls are relatively low (page 24), successful leaps are very infrequent. At these times many fish accumulate in the 'Pot' and provide a spectacle for the public by day and a lure for poachers by night; and in low water provide conditions which could result in heavy mortality in the event of an outbreak of disease.

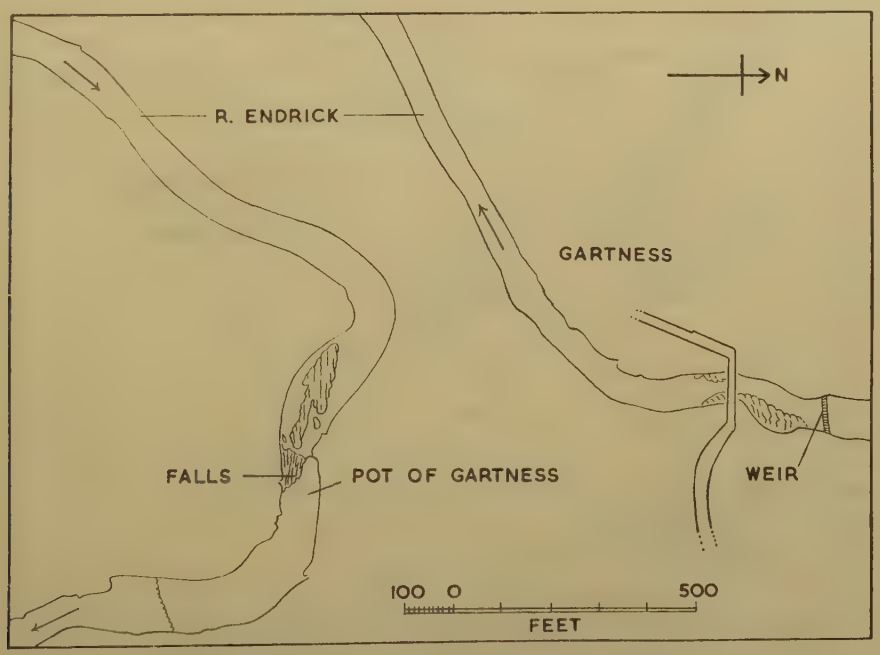

Fig. 8 Plan of River Endrick near Gartness.

The peculiar difficulty presented to the passage of migratory salmonids by the falls of the Pot of Gartness has thus been recognised for at least half a century, but the true nature of the obstacle has never been defined. The individual falls are not high; there is a deep pool below the falls which most observers are agreed is essential (but for different reasons and these will be discussed later); the fish find no further comparable obstacle when they have performed successfully the initial leap—but it is the initial leap that fails too frequently.

The following account is an attempt to define the true nature of these and other similar obstacles in the light of the experiments described above and the observations made on salmon and trout under a wide variety of conditions.

The Pot of Gartness

The situation of the falls in relation to the course of the river presents some unusual features. The River Endrick is approximately 60 feet broad at this point and approaches the fall in a 'reversed S' bend (Fig. 8). This double bend is caused, not by normal meandering, but by the river meeting a large outcrop of hard sandstone and being partially deflected while cutting a course through the outcrop to form an open gorge with steep sides. As a result, the main current flows to the falls on the convex side of the bend where consequently, erosion and cutting back have proceeded more rapidly than elsewhere. Probably due to the unequal rate of erosion, the otherwise regular fall reaches diagonally across the river at an angle of roughly 40°, thereby increasing its length by nearly 50%. Where the main current drops into the pool below, the greater erosion at this place has formed a narrow neck (Fig. 9) bounded on the left bank by a perpendicular wall of sandstone, heavily scoured by the vortices generated by the fall. From bank to bank the jointed blocks and flat slabs of sandstone which form the falls are undercut by the action of the falling water. Above the drop, outcropping ridges direct the flow at high water levels into several channels which, while still directing the main current as before, overflow on the broad platform to form subsidiary falls. The height of the platform varies from about 7 feet on the left bank to 6 feet on the right bank with a narrow central depression about 4 feet above the pool below. At low

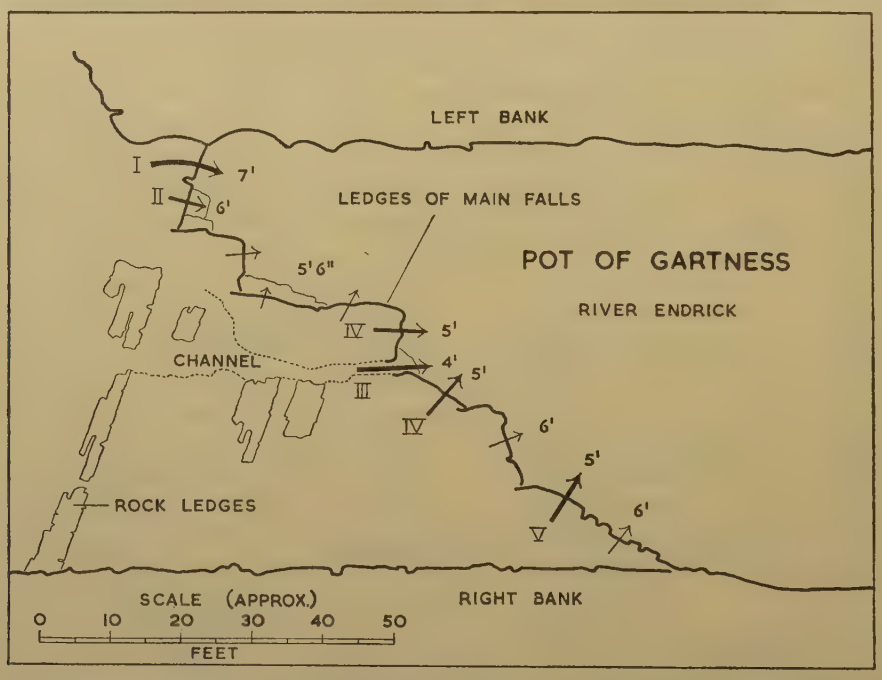

Fig. 9 Diagrammatic plan of the falls at the Pot of Gartness. Arrows indicate relative value of discharge, Roman numerals the sequence of flow and Arabic numerals the approximate height of fall over the ledges.

water levels, the total discharge of the river, often constricted to 12 feet or less, thus drops over the highest fall, while the remainder of the 85 foot-long platform is dry. In addition to a gentle slope from left bank to right bank, the whole rock formation dips more steeply in a downstream direction.

With increasing discharge the water extends over the platform by devious paths to form a number of separate falls, the sequence of flow and relative discharge of which are indicated in Fig. 9. In full spate, the platform is completely submerged, but the individual falls are readily distinguished by the locally heavier flow, and it is to these falls alone that leaping is directed. Salmon and trout have not been observed to give their attention to more than two of the falls at any given stage of the river and usually leaping is evident at only one. However, as will be described below, the choice of a particular route varies according to the discharge over the falls and the relative size of the fish.

Leaping Behaviour

Throughout the summer of 1959 the river level was almost continuously affected by drought conditions and very few salmon and trout were able to pass the falls. During the greater part of the time the river was constricted at the fall within a space of about 6 feet through which the total discharge passed, dropping from a height of 6 ft 6 in. to the pool below (Figs. 9, 10). Owing to the downstream dip of the fall platform, the velocity of the water was increased considerably giving a shooting character to the crest of the nappe which, however, owing to the height of fall, became almost vertical as it struck the pool.

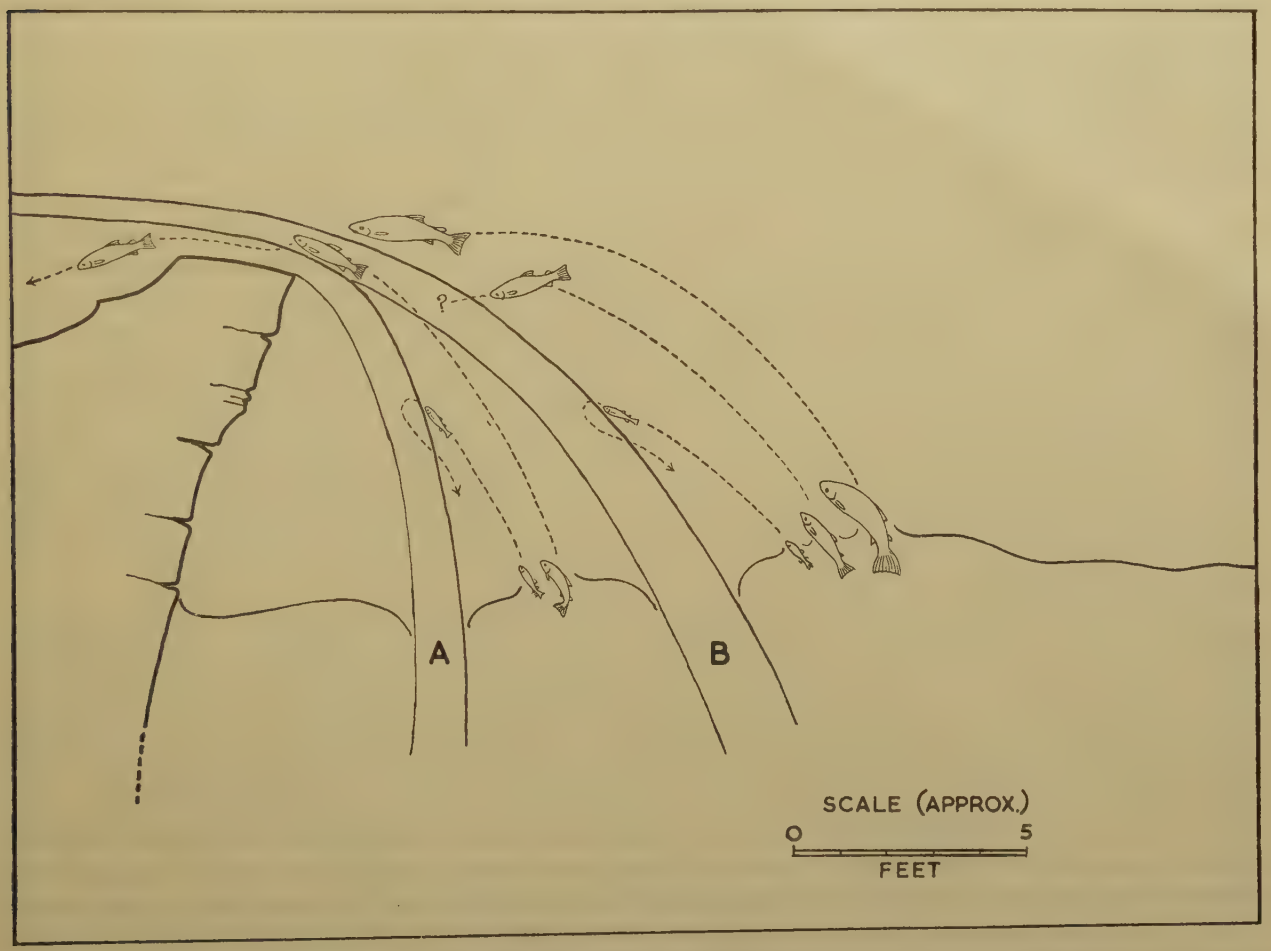

Fig. 10 Sea trout, brown trout, salmon and salmon parr leaping at main fall during low (A), and medium (B) discharges.

During several successive visits while these conditions obtained some parr and small sea trout were seen leaping spasmodically without success. These leaps seldom attained a height of more than 2 feet and, in the light of later performances during freshets and spates, the impression remains that the motivation was very low.

With an increase of two or three inches in river level another fall came into operation alongside No. 1 (Fig. 9). This fall is stepped about 2 feet from the top and its discharge converges with that of No. 1. Fish seldom leap directly here, but misleaps from No. 1 sometimes land on the step, from which they are invariably swept. When this fall begins to operate however, the increased discharge at No. 1 becomes attractive for sea trout up to about 14 in. (36 cm.) in length, as well as the smaller fish (Fig. 10A). The river, however, under these conditions is still at a low summer level and there is little doubt that this fall becomes attractive to these fish owing to the concentration of the river flow into one narrow section. By early October, when similar conditions and similar behaviour of the fish were observed, a number of large salmon were congregated in the pool, lying in regular formations in relatively shallow water about 50 feet from the fall. Not one of these fish moved forward to attempt what could have been for them an easy leap. The leaping behaviour of the trout and small salmon at this time was observed closely and was found to agree in every respect with that described above for the smaller fish in the laboratory experiments. The behaviour of the water was also comparable, as observed from above, and the 'hump' caused by the upward current was clearly identified. As in the laboratory tests, all the fish leapt from the apex of the 'hump' in front of the 'toe' of the fall and the larger ones attained the necessary height of about 7 feet with apparent ease. At the same time salmon parr and immature sea trout (10 cm. to 15 cm.) accomplished consistently a clean jump of 3 ft 10 in. from the surface of the pool but, as they struck the falling water, were immediately hurled downwards again.

Over a period of 30 minutes (14.30 hrs to 15.00 hrs) the fish were leaping at an average rate of 7/min., recorded by stop watch and tally recorder. A similar count obtained over a fifteen minute period at 16.00 hrs showed a decrease to 3/min. Before, after and between these periods many other leaps were observed.

Of the larger fish, one in three made successful leaps at this fall (at this time) but it is not known certainly that these fish were successful at the first attempt. The ascent into the short pool above the fall was however accomplished, in all cases, with considerable difficulty owing to the chute-like platform leading upstream from the crest of the fall which caused the water to pass the lip with a very high velocity. Fish that leapt with relative ease to attain the necessary height re-entered the water to encounter immediately this high velocity. In general, all fish that re-entered the water at the crest belly first were at least able to maintain their position for a few seconds and some, particularly the larger individuals, made a slow but steady progression into the safety of the pool above. Others, after maintaining position for two or three seconds with only minor vertical movements, abruptly gave up the struggle and were swept rapidly downstream. Every fish, irrespective of size, from the smallest parr to the largest salmon, that re-entered the water at the end of the leap nose first was immediately hurled downwards again. While this type of entry was not very common at this stage, at much higher discharges it became the rule and no fish was then able to pass over this fall.

Observations on the behaviour of the fish at the foot of the fall were difficult owing to the turbulence and masses of foam on the surface and the actual 'take off' could seldom be observed clearly. Shoals of fish, however, were seen radially disposed just beyond and to the sides of the 'hump', actively maintaining position about 12 inches or so below the surface and showing the characteristic 'head down' attitude noted in the laboratory. Every few seconds one or two fish could be seen to move forward into the turbulent zone and immediately afterwards a leap would take place or a fish would appear raised bodily to break the surface and be carried forward to submerge again at the toe of the fall (Plate 4). This latter observation was of special interest for it demonstrated the force of the upward current and the relatively passive reaction of the fish entrained. It has been observed in the field and in the laboratory on numerous occasions when the temptation to ascribe to the fish a motive of inspection and estimation of the leap had to be resisted. Lamond (1916) for instance, describing the leaping of sea trout, states 'I have spent many hours watching the fish thus leaping, and have not the least doubt that before making a leap at the obstacle sea trout carefully take their bearings. If watched closely for some time a particular

fish will be seen poising itself amid the foam of the pool, sometimes the head alone, but often the head and pectoral fins, being out of the water, facing the fall. Then the fish disappears for a few seconds and one may expect it, and not another fish, to be the next to leap.'

In view of the consistency of attainment of the correct height it seems probable that the fish makes some estimation of the height of the fall, but no evidence was obtained in the laboratory that this short preliminary excursion above the surface always preceded a definite leap. At Gartness, one fish, marked by a damaged head, was observed to jump at a fall, which had become impassable, at a rate of 7 times in 15 minutes without appearing, as described above, between jumps, though other fish were doing so. A more likely explanation is that the breaking of the surface is involuntary. At the foot of natural falls, owing to the pulsating fluctuations of the velocity, the hydraulic 'hump' is never stationary, though remaining within a narrowly circumscribed area, while its amplitude reflects that of the fluctuating flow. Misleaps, therefore, of which this 'preliminary' emergence is probably a weakly activated example, may possibly be due to a failure of synchronisation of the leap to the peak amplitude and position of the 'hump' and this theory is supported by observations at more regular falls and at the weirs in the laboratory where such failures were rare.

At the beginning of a leap the turmoil at the surface of the pool partly obscures the body of the fish as it rises in the air, but in many cases a strong flexion is seen. At a height of about three feet however, when clear of the water, the body flexions cease and the fish assumes the aspect of a rigid projectile describing an arc to the crest of the fall. As it passes upwards through the air all fins are extended, but, excepting the caudal fin, not rigidly so. The tail and fully extended caudal fin are now vibrating visibly and audibly, the characteristic rustling sound from a large fish being clearly heard at close quarters above the deeper note of the tumbling waters. In this manner the fish strikes the rounded crest making first contact ventrally, with the body almost parallel to the water surface, but with the head, mouth, lower jaw and pectoral fins clear. Immediately following the impact the body totally submerges, already aligned to the direction of flow, and the still vibrating tail, with no perceptible sudden change of frequency, resumes its function as a propeller. (In this connexion it appears possible that certain hydraulic phenomena may give immediate assistance to the fish at this critical stage and these will be discussed below).

The above observations, thus far, agree closely with those for the experimental falls (p. 15). At the Pot of Gartness, however, the high velocity above the crest resulting from the downstream dip of the rock, formed a chute of greater or lesser extent which demanded the utmost effort of the fish immediately following the leap and was the cause of the great number of failures. At fall No. 1, when leaping first commenced, the length of the chute above the fall was only about 3 feet and the observer could approach within a short distance of the leaping fish. The observations on the behaviour of the fish following the initial leap were further facilitated at one period by the high velocity causing the water to be banked against the smooth rock wall on the left bank thus providing a slightly deeper channel for the fish at this place with a smooth and transparent surface at an angle that permitted a lateral view of the fish.

It was thus seen that all fish, whether destined to ultimate failure or not, on striking the crest were immediately impelled forward to make progress of from six to twelve inches against the strong current. In all cases there was then a momentary check, but from here the larger fish (25 cm. to 36 cm.) slowly progressed upstream to enter the pool above. Smaller fish, after the check, sometimes remained for up to 3 seconds swimming vigorously but making no progression. Eventually, at the point when they began to lose ground, the fast swimming action gave place suddenly to a more sinuous body and tail movement and the fish were swept downstream. Some of the larger failures were observed to pass over the fall head first, but owing to the speed of the movement it is not known whether this was the result of positive orientation or chance. The smaller fish demonstrated every possible position relative to the current as they hurtled back to the pool.

As already mentioned, the above observations were made with the river running at summer levels, the concentration of the total flow on the one side stimulating and facilitating the passage of fish up to about 36 cm. in length while larger fish, salmon and sea trout, lay inactive near the tail of the pool. At this stage the falling water entered the pool almost vertically and the 'take off' point for the leap of 6 ft to 7 ft was located about 5 ft downstream from the crest of the fall (Fig. 10A). At higher river stages,

however, the increasing discharge and velocity caused the water to shoot beyond the crest of the fall and plunge into the pool at a distance of from 8 ft to 10 ft downstream (Fig. 10B).

While the volume and velocity of the water increased it became more and more difficult for the smaller class of fish to reach the crest of the fall and eventually failures became total. At this stage it was noted that the maximum height attained by individual leaps was about the same as before, but at a distance of several feet from the crest, with the result that the trajectory of the fish through the air curved downwards to meet the falling water at a sharp angle below the crest. The fish thus entered the high velocity jet head foremost and was immediately hurled downstream. In many cases the fish was thrown backwards into the air and it was observed that when this happened the vibration of the tail ceased and waves of large amplitude travelled slowly down the body. Failures to attain the crest were without doubt attributable to the horizontal distance, about twice the vertical height, that it was necessary for the fish to accomplish.

Before this fall became completely impassable owing to the increasing weight of water, the salmon and larger sea trout, which hitherto had remained placidly at the tail of the pool, began to show evidence of stimulation. In ones and twos they broke the surface, still near the tail of the pool, and an occasional fish leapt vertically two or three feet into the air. About twenty minutes later the first large fish made an unsuccessful leap at the fall and was followed by an increasing number of other unsuccessful attempts. Many of these attained the crest, but the chute above was too strong and, owing to the shortness of the

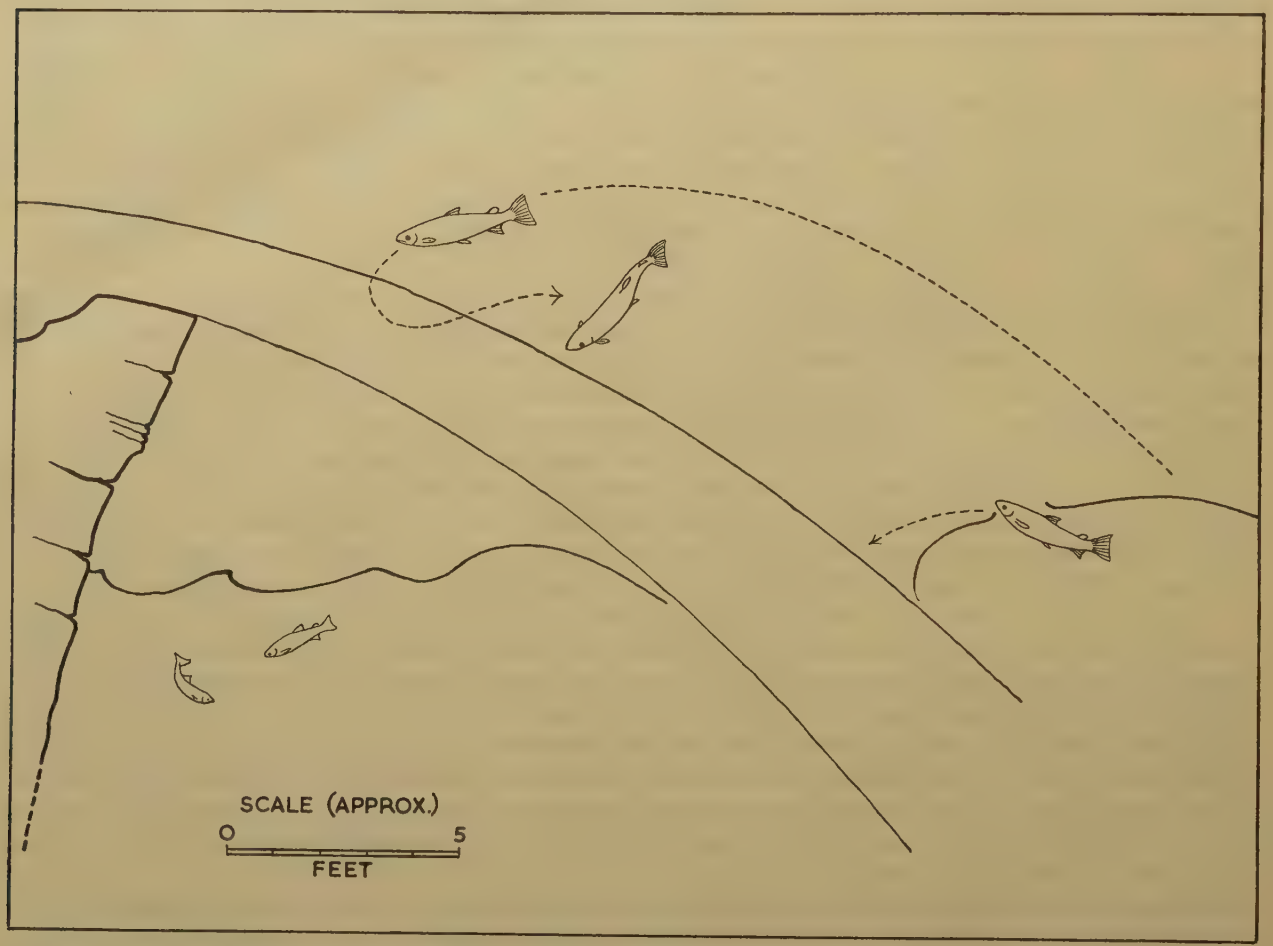

Fig. 11 Abortive leaps of large salmon at main fall during high discharge and passive entrainment of another in the roller of the standing wave. The smaller fish displaced or leaping elsewhere.

pool above, too turbulent for any fish to maintain its position even momentarily. A little later, with a further increase in discharge over the fall, the previous observations on the behaviour of the smaller fish were repeated: from a 'take off' point now about 20 ft from a barely distinguishable crest, the larger salmon described an arc to descend head first to the rushing water and be thrown again into the air (Fig. 11).

With the rising flood the water commenced to spread over the rest of the platform and fall No. III came into operation. By the time the first salmon had attempted fall No. I the smaller trout and parr were already leaping here, but owing to a short submerged ledge immediately below the fall, reaching the necessary height with difficulty. Although only 4 ft in height, this fall is quite as formidable an obstacle as No. I. The water is led to this, the lowest edge of the platform, by a three foot wide channel, partly natural and partly man-made, in which the water flows rapidly and shallowly to shoot over the edge of the fall. As the flood extends to overflow the rocks (IV) on each side of the channel the falling water overshoots the submerged ledge and attracts most of the leaping fish, while the activity decreases at fall No. I.

At this stage, before the platform becomes totally submerged, all sizes of fish, except the smallest parr, have little difficulty in leaping on to the platform, but owing to its extent and the shallowness of the flow, they are forced to swim for several yards until eventually the passage of the larger fish is blocked by a ledge of only 12 inches or so in height. For a great number of years it has been usual for river watchers to be in attendance here to assist the fish into the pool above. Smaller sea trout and parr are able to pass through without much difficulty, finding shallow runnels between the ledges through which they are able to swim. At full flood it is doubtful if any fish can pass the fall except by chance, for although leaping may persist near the right bank (V), the multiplicity of water falls converging, diverging and impinging on each other presents a scene of confusion and results in much erratic jumping and damage to fish.

The above sequence of events has been described as it occurred in the river rising to high spate from a low summer level. In reverse order the same sequence was observed as the river level dropped back to normal. It was not always possible to follow the sequence throughout. The onset of darkness always caused leaping to end or a flood did not attain maximum proportions before falling back again. But at each visit when leaping was observed the fall which was the main objective of the large or the small fish (as defined above) could always be correlated, according to the observed sequence, with the particular stage of the river level. It was thus confirmed several times that there was an optimum discharge at each individual fall that was related roughly to a range of size of fish which was attracted solely to it and, as the discharge increased or decreased, so did the range of size of these fish, irrespective of species. Thus at fall No. I large salmon and sea trout could be seen leaping unsuccessfully, while, concurrently at fall No. III, very much smaller fish were meeting with some success. In no case (except for the salmon parr) was the height alone of the fall a serious obstacle and an estimated 90% of failures was due solely to the very unfavourable conditions upstream from the crest.

DISCUSSION

The Route over the Obstacle—'Selection' and Timing

The observations and experiments have shown that the behaviour of migrating salmonids, adult and juvenile, when faced with a barrier or obstruction, can be correlated directly with the hydraulic conditions obtaining in the river channel. The laboratory experiments demonstrated the attractive power of stream velocity and showed that the fish were guided to the vicinity of obstructions by a positive rheotaxis, whereas in static water, except for one interesting exception which was probably due to conditioning (p. 20), the topography and alignment of the channel provided no clues. These fish will thus locate a possible pathway over an obstruction by their pertinacity in pursuing a course upstream wherever the velocity of the current permits. Even when the velocity is too high for progress to be made they will often persist in attempting a passage over long periods with all the possibilities of exhaustion and damage.

These facts are, however, well known and are the source of the spectacular element wherever salmon and trout encounter barriers to their progression upstream.

Until now no explanation has been available to account for the behaviour of the fish when confronted with a 'choice' of routes or for their leaping activity at one time and not at another, or indeed for leaping behaviour itself. Only in very general terms has this behaviour been related to the volume of river flow at a given time (Calderwood, 1926; Menzies, 1934) and the tendency has sometimes been to regard leaping as 'a last resource' of the fish (R.C.F.P., 1942).

The present work has shown that the route taken is fixed before any attempt at passage over an obstruction, that the selection is a general one for all fish within a given size range and that, once decided, the route is persistently attempted without deviation even when failure is general and prolonged. Such efforts may continue until the pattern of river flow changes or until the advent of darkness or turbidity. At the Pot of Gartness the availability of a variety of routes, each of which was used exclusively according to a particular level of river flow, demonstrated first, the fact of 'selection' and secondly, that the discharge of water over the 'selected' route was not always the greatest (or the least) available. At low water levels large salmon remained inactive in shoals at the tail of the pool while a smaller size range of salmon and trout leapt successfully at a single waterfall over which the total discharge of the river passed. As the discharge over this fall increased with rising river level, the large fish became active while the smaller fish moved across the pool to a subsidiary fall, actually lower in height though it proved to be a more difficult obstacle to these fish.

It was evident that the increased volume of water over the first fall was the attraction for the large fish, for they persisted in their attempts to surmount this fall (which earlier was passable to the smaller fish), although with practically no success due to the now chute-like crest of the fall. There can be little doubt that, had the larger salmon been stimulated to attempt the leap concurrently with the earlier efforts of the smaller fish, their leaps could have been 100% successful: at least not less successful than those of the trout.

Thus it appears probable that the signal that stimulates the fish to move forward preparatory to the leap is related to the impact of falling water on the surface of a pool. As the force of the impact varied with changing river discharge so also did the relative size of the fish that responded. In the laboratory, with a constant discharge through the flume, leaping commenced only when the unstable nappe sprang freely from the crest of the weir to make impact with the surface of the pool instead of flowing smoothly down the face of the weir (p. 11), and frequently the leaping reaction could be induced in a static pool by pouring water from a height on to any part of the pool surface. All these observations indicate the area of contact of the falling water as the source of the stimulus which may be communicated to the fish as pressure waves or elastic waves. It is also evident that this stimulus varies with the force of impact and that the threshold value at any given time varies directly as the size of the fish.

The Nature of the Stimulus

The nature of the stimulus, however, requires further investigation. Crude attempts during the present study to transmit sound waves or other vibrations through the water by various mechanical devices appeared only to alarm the fish, but the impact of falling water was invariably attractive and frequently stimulated leaping behaviour in the laboratory as much as 15 to 20 feet from the point of impact, and up to 50 feet in the river. Little is known regarding the sensitivity of salmonids to vibrations but the ability to hear has been established for many other species and the localisation of the source of low frequency vibrations has been demonstrated in a cyprinid by Kleerekoper and Chagnon (1954). These authors review the problems of hearing in fishes and emphasize the technical difficulties of experimentation in this field. Lowenstein (1957) provides lists of teleosts in which hearing has been reliably demonstrated with data for the range of tone perception and tone distinction. The range is greater for fishes which possess Weberian ossicles (Ostariophysi) than for other teleosts. For example, the frequency range of tone perception for the minnow (*Phoxinus phoxinus*, Ostariophysi) is given as from 16 to 7,000 c.p.s., while for the eel (*Anguilla anguilla*, non-Ostariophysi) it is 36 to 650 c.p.s. No data are available for salmonids but it may be assumed that the perceptual ability lies somewhere between these ranges with a

tendency towards the lower. Sound perception and pitch discrimination are usually closely allied and this ability may well account for the observed behaviour in the natural river. If we postulate that the choice of a particular route is related to a certain intensity of sonic or other vibration, or that the response to a change of pitch following an alteration in the discharge over the falls causes the hitherto passive fish to move upstream, this explanation is not incompatible with the observed behaviour of both fish and river. Haempel (1911) studied the responses of fish to underwater tones and concluded that Salmonidae and Cyprinidae have the ability to respond and also showed that younger (smaller?) fish have a stronger ability to respond than older fish. In the present work it was seen that leaping in the smaller fish always preceded leaping in the larger in a rising river level and could be correlated with a change in the value of the stimulus rather than with its duration. These fish, large and small, always responded to what was no doubt an optimum stimulus and were led to a particular source accordingly. As was shown above, this usually resulted in a separation of size groups among the leaping fish.

Lowenstein (1957) considers that the evidence in favour of sound perception among teleosts is impressive and 'makes the assumption of a well defined biological significance of hearing inescapable'. A very high performance, or low threshold of response, however, could well be a disadvantage to non-Ostariophysi such as salmon and trout which may spend a great part of their lives subjected to a continuous, fluctuating 'background' of underwater vibrations. The assumption of a lesser performance in an environment which may alternate rapidly from a babbling brook to a raging torrent is in keeping with the observed behaviour and could provide an explanation for many of its aspects.

Superaeration

It is generally accepted that low discharge in a river is an inhibiting factor while superaeration may reduce the effectiveness of an increased discharge. It is also noted that the latter condition loses its importance with an increase of temperature; when it occurs in the cold waters of spring it is a complete barrier but may be frequently passed in summer and in autumn. There appears to have been little consideration given to this phenomenon by fishery biologists beyond an acceptance of the fact of its inhibiting effect on upstream movement, whereas its importance in the engineering field has been increasingly recognised in recent years (Leliavsky, 1957). It would, therefore, seem profitable to consider the physical nature of superaerated water in the light of the researches of the hydraulic engineer and to attempt a correlation with the known behaviour of migrating fish.

In a river or artificial channel where the flow of water is allowed to accelerate over a sufficient distance air is mixed with the stream and the phenomenon of 'white water' occurs. The volume of air which will become mixed with the water appears to be in proportion to the velocity; in other words a velocity of 10 ft per second would entrain 10% of air by volume and a velocity of 40 ft per second would entrain 40% of air by volume (Hall, 1943). According to Straub and Lamb (1953) 'a characteristic roughening of the water surface immediately before the appearance of "white water" can readily be seen on most free surface installations where self aeration occurs . . . . The depressions or open pockets of air at the interface above the densely underlying fluid and the spikes or projections of water mixture projecting into the air are of varying dimensions and spacing in seemingly random occurrence. This violent agitation of the interface between the mixture and the air serves to entrap quantities of air which are then broken into bubbles of a size that presents a balance between the work of agitation of the liquid and the surface energy of the resultant bubbles. *Thus, the air bubbles in water are approximately spherical in shape and close to the same general size for a given set of flow conditions*'.*

When applied to the flow of the water in an open channel the term 'high velocity flow' means flow at a velocity greater than the critical, or the wave velocity for that particular depth (see p. 12). The velocity of a surface wave is the velocity of propagation of a disturbance: that is, the force through the flow. These waves are not initiated simply by the high velocity of the flow. Initial disturbances are necessary and in rivers and artificial channels the sources of such disturbances are, normally, roughnesses in the channel and local irregularities, which affect the level of turbulence (Knapp, 1943; Hall, 1943). Continuous air entrainment associated with superaeration or 'emulsified flow' results immediately after these

*Writer's italics.

disturbances give rise to turbulence layers, the depth of which, when they coincide with depth of flow (Lane, 1939), results in the characteristic roughening of the water surface.

Under these conditions very large amounts of air can become mixed with the water, in some cases up to 60% (Hall, 1943). This results in a high degree of 'bulking' of the flow in the pool beneath with the result that the depth of water downstream from the point of impact may be 20% to 50% greater than for non-aerated flow (Jevdevich and Levin, 1953). It will thus be realised that the impact of a given discharge over a fall, weir, or rapid, will vary, not only with the height (or static pressure), but with the nature of the bed over which the water flows before dropping. If the irregularities of the channel are such as to induce turbulence the amount of air entrained will increase accordingly and the force of the impact will be correspondingly lowered. It is evident that in extreme cases of insufflation the density of the mixture will be very much reduced and will detract from the propulsive power of the fish tail (as has been already suggested by earlier writers) and diminish the buoyancy of the fish; it may also reduce or otherwise alter the stimulus. This alone may suffice to account for the hesitancy during the cold season when the rate of metabolism is low. It is equally well known, however, that under warmer conditions the fish will ascend through the 'white water' more readily and, while this agrees with the theory of an increased rate of metabolism, it may also owe much to the higher intensity of the internal motivation or 'drive' (Thorpe, 1951) as the gonads approach maturity. An increased activity is very evident in salmon and trout near to spawning time when gravid females perform the leaps at Gartness and elsewhere as frequently and as easily as the less encumbered males. If 'cold white water' is simply a barrier because the density of the mixture is too low to provide adequate resistance to the flexing of a fishes' tail, the inference must be that the fish is somehow 'informed' of this disadvantage *before* it attempts to make the passage, for no accounts of attempts to leap under these conditions are available, nor have any been observed by the writer.

It is therefore suggested that a more probable explanation of the barrier effect of superaerated water is the high threshold of response due to the low intensity of the drive in the cold early months of the year, coupled with the weak signal derived from the impact of the water. If the stimulus to leap should prove to be the shock effect of vibrations or elastic waves, such phenomena will undoubtedly be damped by the presence of large quantities of compressible air bubbles in the relatively incompressible water. In addition, aeration also reduces the force of the impact when water falls from a height and at very high falls the impact on the pool beneath may be very much reduced, or the energy almost completely dissipated, due to the transformation of the aerated water into mist. At falls of medium height, but beyond the range of leaping power of the fish, the impact produced by the emulsion of air and water may be so reduced that a false clue to the actual height is possibly obtained by the fish. The writer has observed numerous salmon leaping simultaneously and continuously over a period of hours from a deep unobstructed pool and attaining an almost constant height of leap (4-5 feet) at a high, impassable fall of around 30 feet; but the height attained here was much less than the recorded maximum at other passable falls.

It is necessary at this point to define the second important type of aerated flow found in the vicinity of waterfalls which, in the writer's experience, is habitually confused with that described above.

Michels and Lovely (1953) have described and classified the types of flow occurring in natural and artificial channels according to the degree of aeration: the above description agrees closely with the flow described by these authors as 'emulsified'. It is this emulsified flow which has been termed 'white water' and which appears to be a barrier to the passage of migrating fish. At the foot of many waterfalls, however, violent air-water mixtures can be seen occurring as a 'boil' on the surface although the falling water may be relatively non-aerated. This is the location of the 'hump' previously described (p. 13) and it was seen that, instead of hindering the passage of the fish, under certain conditions it could be of marked assistance. This 'boil' or 'hump' extends irregularly through a portion of the water in a pattern which depends on its boundaries and on the inflow and outflow conditions. The air is apparently enveloped or drawn in at the free surface of the turbulent impact zone existing between a rapidly moving stream and a slack or comparatively slowly moving body of water; air may also be entrapped at the upstream surface of the comparatively slowly moving body of water by the rise, dispersion and fall of water particles which possess large vertical velocity components. The air thus entrained may be recirculated in a vertical roller

Plate 5 Female trout excavating the nest. The pectoral fins, distended and extended headwards, act as brakes and allow the force of the action to be directed downwards and to the rear.

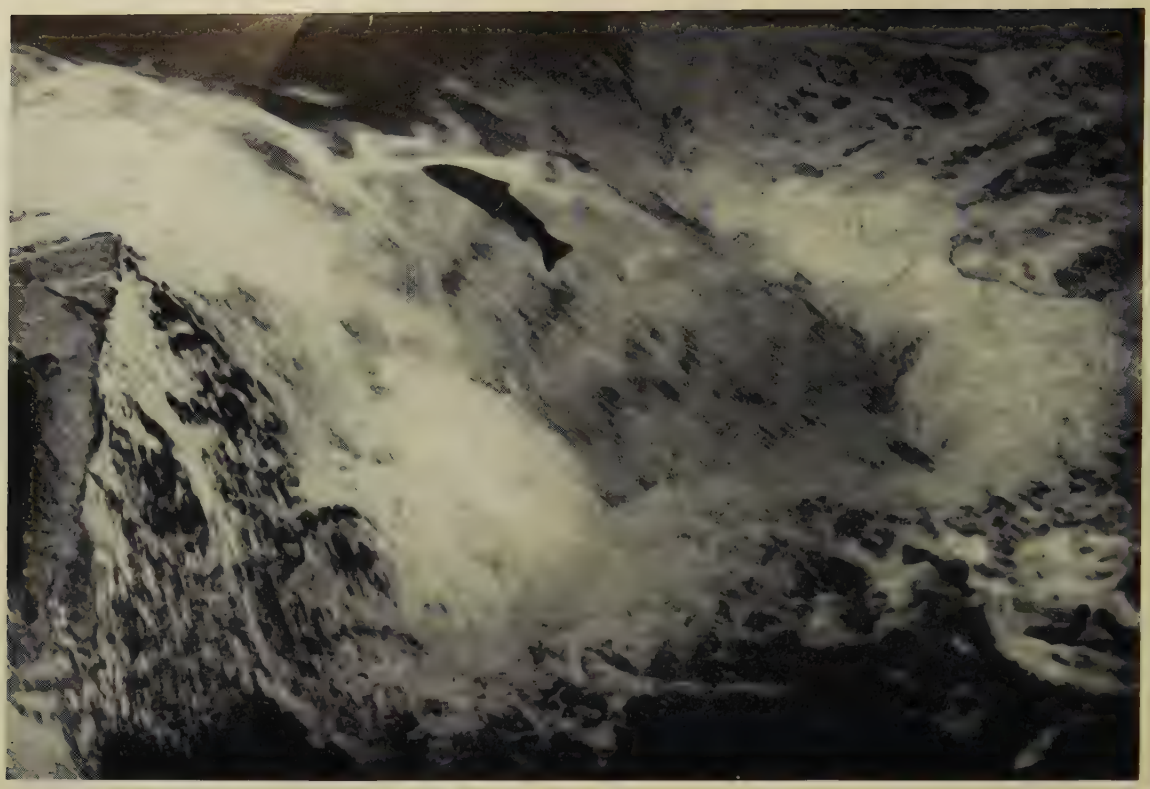

Plate 6A Leaping salmon.

Plate 6B Leaping salmon just after 'take-off'.

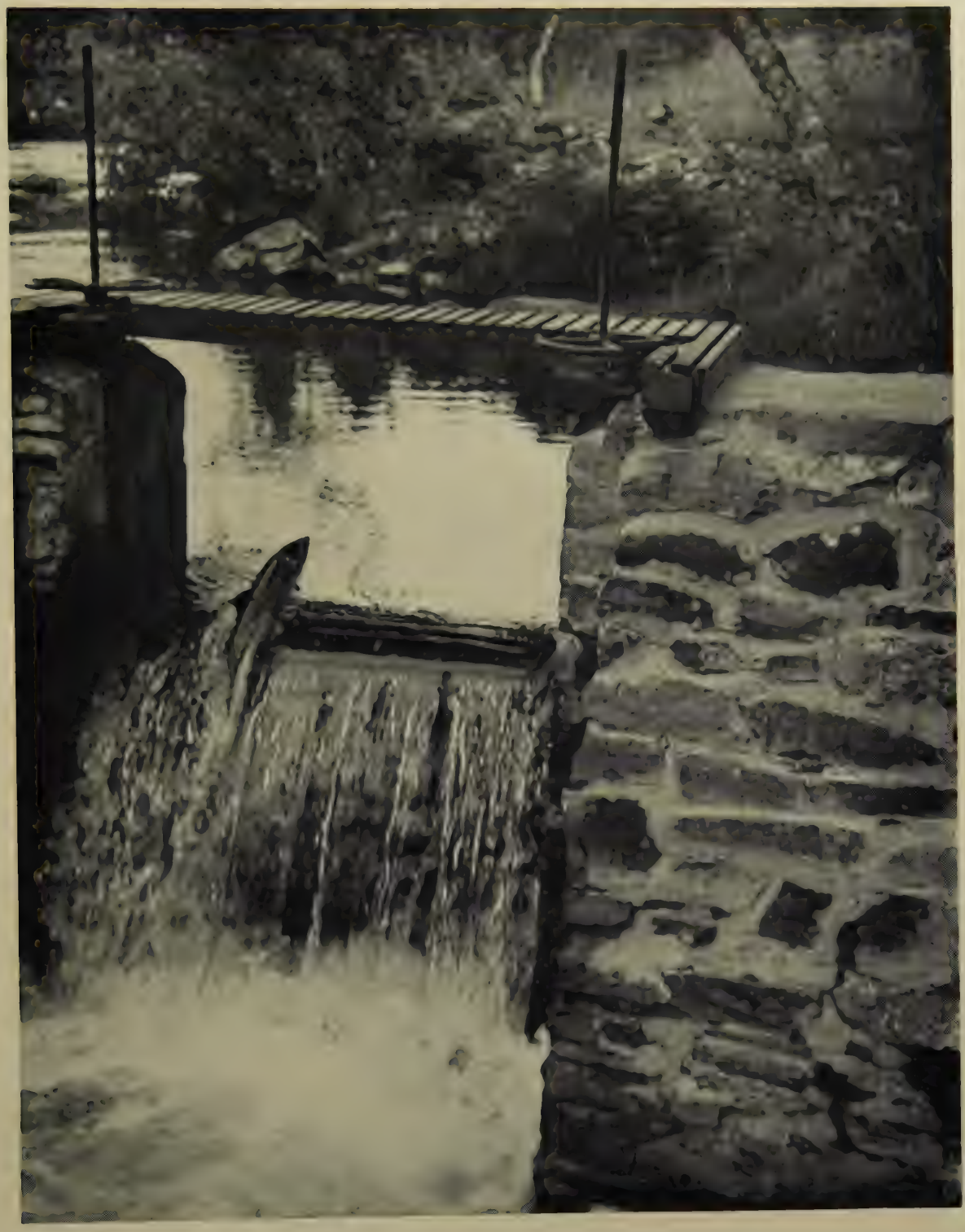

Plate 7 Leaping salmon at sluice and track of preceding fish.

(p. 16) but generally it escapes gradually in the direction of reduction of turbulence. In this case the depth of flow is locally increased but diminishes as turbulence is damped out and air escapes. These conditions are found wherever a high velocity jet falls into a natural pool and the flow is characterised by large vertical components of velocity and high local energy gradients. Beyond the zone of impact lateral velocities are generally small (Michels and Lovely, 1953).

The mixture of air and water formed by impact in a natural pool seldom warrants the term 'emulsion' and the condition is distinguished by the larger and irregular size of the bubbles and their quicker release upwards. In the laboratory channel it was seen that while some bubbles made several circuits in the attenuated roller a large number escaped directly upwards, assisted partly by the upward current. According to Knapp (1943), 'The depth of penetration of air below the surface will depend on the size of the bubbles and the level of turbulence. Large bubbles will penetrate less than small ones.' This was confirmed in the laboratory pools and, while observations could only be made on surface effects in the field, it was observed that when leaping stopped at a particular fall, coincident with increasing discharge and turbulence, the water surface had become frothy owing to the smaller size of the individual bubbles.

As already mentioned, the above observations on the behaviour of water and air mixtures support the theory, on purely physical grounds, that the fish orientates towards a 'noise' or disturbance. It has been shown that the quantity of air and the size and distribution of the bubbles are related to definite conditions of flow which tend to recur always at the same discharges. Emulsified water and air being more or less independent of impact conditions (as defined above) will vary less with discharge and the thick curtain of closely-arranged, fine bubbles would almost certainly produce, or, by absorption or reflexion, reduce the vibrations to a constant unmodulated 'note' of low intensity. On the other hand, the lesser entrainment produced by 'black water' striking a pool is proportional to the force of impact and the 'note' will vary accordingly. The mechanism therefore exists to transmit a variable signal (or stimulus) to a fish whose internal motivation is tuned to respond differently at certain seasons, or not at all at others, to react to an appropriate signal or to give no response to an inadequate one. The relative effectiveness of reflexes on responses of this nature has already been shown to be influenced by internal factors (von Holst, 1950). It is also quite possible for the human ear with experience to distinguish different levels of discharge in a river by the sonic vibrations conducted through the less efficient medium of the air.

The Importance of Pool Depth

Owing to the turmoil created on the surface of the pool by the impact of the falling water, it is almost impossible to analyse the movements of the fish immediately prior to the leap, but in the laboratory all leaps commenced from a point near the surface and, in the natural river, aggregations of active fish were seen radially disposed near the surface in front of the area of impact into which they darted one by one from all sides to break the surface on the apex of the 'hump' and leap towards the crest of the fall, or to be carried passively forward on the surface into the falling water (p. 26). No fish was ever observed in the laboratory, or in the field, to approach from a distance, laterally or vertically, and perform a leap without a waiting period of long or short duration. The location of a stimulating fall is always marked by the congregation of active fish in the near vicinity. When no leaping is taking place all fish are passively distributed in relatively tranquil water, chiefly towards the tail of the pool. The close proximity of areas of extreme turbulence and relative tranquillity is clearly defined by the disposition of the active fish.

In the laboratory experiments it was shown that the behaviour of the falling jet of water as it enters a pool depends to a great extent on the depth of the pool. If the pool is shallow the jet strikes the bottom and is deflected, with its velocity virtually unchecked, for a distance downstream. Depending on the characteristics of the downstream channel, a standing wave (or hydraulic jump) will form at a distance from the fall and it was shown that leaping took place at this point and no other (p. 12). It is known that at this place there is an abrupt loss of energy. Oversubmergence of the jump will cause the undershooting jet to persist for a greater distance downstream (Moore, 1943). When a pool becomes very deep in relation to the height of the fall the jet flows along the surface and may continue, as in the first case,

virtually unchecked to the end of the pool. Depending again on the channel characteristics (presence of obstructions, etc.), a standing wave may or may not develop. Fish attempting passage in the absence of a standing wave will endeavour to swim all the way through the pool against accelerating velocity. When a succession of such conditions is encountered in unbroken sequence, as, for instance, in the conventional fish ladder, the fish inevitably must expend considerable effort. The same remarks apply to fish passes of the pool type with submerged orifices.

The experiments showed clearly, however, that when the ratio of height of fall to pool depth approached a value of 1:1·25 the standing wave became submerged at the toe of the fall and brought the leaping fish close to the obstruction. It was also found that this ratio was similar to that of falls and scour holes in the natural river.

The standing wave is a phenomenon which has been known and studied for over a hundred years, but the erosive effect of which has been understood only relatively recently (Leliavsky, 1955b). According to Leliavsky, 'The erosive effect of the standing wave is closely related to its action as an energy destroyer, for the energy which we describe as "destroyed" is used—at least in part—in generating the excessive vorticity, which in turn causes scour. On the other hand the loss of energy in a wave is also capable of being visualised as a "shock" effect.'

Hydraulic engineers, particularly those concerned with the construction of barrages, weirs and dams, having perforce to consider these erosive effects, have devised various anti-scour devices to protect their works from damage, the majority of which seek to position the standing wave at a designed distance from the weir or dam. Probably the most important of these works have been concerned with the barrages and irrigation works of Egypt and India where, unfortunately, the passage of migratory fish was not a factor to be considered. As a result, many minor obstructions, and probably some larger ones also, have been designed on the same principles and erected in rivers whose stocks of migratory fish are of some importance.

It was, however, of considerable interest to find some confirmation of the present work in the experiments of an irrigation engineer in India, quoted by Parker (1925), 'Dyas found experimentally that a bottle was not smashed when passing over the fall when δ was greater than $\sqrt[3]{d}\ \sqrt{h}$ when δ=depth below bed level, h=height of fall, d=the full supply depth of the canal.' There is here a similarity of design with the experiment with the table tennis balls described above (p. 16), and the formula agrees fairly well with the depth of the natural scour hole. A 'stilling pool', 'water cushion' or 'cistern' designed accordingly, was used to dissipate the energy of the falling water, but the method appears not to have been widely adopted in this form outside India. Leliavsky, (1955b), considers that '. . . broadly speaking, the stilling basin, if opposed to various other devices intended for the same objective, represents a rather inexpensive, economical solution of the energy dissipation problem.' The modern modifications of this system, however, which utilise relatively shallow basins are quite impassable for salmon and trout.

It thus appears that the conditions vainly sought after by the early designers of fish passes, i.e. reduction of velocity and suppression of superaeration, are fulfilled *only* when the jet strikes almost vertically downwards from a smooth crest. Compromises such as the use of submerged orifices reflect an approach towards this solution but stop short of the logical conclusion as shown in the following statement from the Report of the Committee on Fish-Passes (1942, p. 55); 'If the orifice is inclined downward the floor of the pool takes the place of the deflecting plane, and this leads to a more rapid velocity-reduction than if the orifice is horizontal. A very much shorter pool can then be used.' As we have seen, the simplest and most effective way of attaining velocity reduction is to incline the jet towards the vertical so that it strikes the surface of the pool at right angles.This was also decided experimentally by Hom-ma (1953) who states: 'The conclusions reached were that free fall generates no distinct zones such as are observed in submerged jets. The rate of deceleration is much larger in free fall than in a submerged jet; the difference is especially remarkable in the case of vertical penetration.'

Discussing the dissipation of energy in a 'stilling basin', Jevdevich and Levin (1953) state: 'the experiments show that the role of depth in a stilling basin is greater than that of its length.' The hydraulic engineer, however, must have been seldom concerned with the necessity of constructing stilling pools in close succession as demanded by the requirements of fish passes. As a result, the length of the pool was a

secondary consideration as long as it confined the erosive vortices and, for reasons of economy, was made as short as possible. When these otherwise satisfactory designs were applied to fish passes fresh difficulties arose however, which are possibly responsible for the *cri de cœur* '. . . but no two pools built to the same specification seem invariably to re-act alike: water is a queer subject to handle.' (Menzies, 1934). The present experiments, however, have suggested that if the outflow characteristics are similar to those of the inflow, a certain uniformity is the natural result when the system is designed to cope with the maximum discharge. The depth of the stilling pool, or scour hole, should be such as to ensure an equilibrium between the energy of the falling water and the energy destroyed or dissipated in the hole, and the end of the pool should be sufficiently distant to ensure that no gross turbulences are carried over to the next pool. If these conditions are satisfied for maximum discharge superaeration cannot take place and lesser discharges have no effects on uniformity. The maximum energy of fall, designed for the optimum stimulus for leaping, must be dissipated as nearly as possible below the point of entry in order that (*a*) the uplift will be available to the fish, and (*b*) that the flow into the succeeding pool will have a minimum of turbulence. The jet should therefore be as vertical as possible to ensure these conditions. In falls of surmountable height, however, there will normally be a horizontal component in the velocity of the water which will place the location of maximum lift at the downstream side of the jet, i.e. at the most advantageous point for the fish approaching for the leap.

Orientation of the Leap

The remarkable accuracy of the actual leap has been discussed in the context of the experiments and little can be added at this stage of the investigations. The location of the hydraulic 'hump' close to the toe of the fall is of undoubted assistance to the fish in locating the crest of the obstacle. In the laboratory, standing waves at a distance of about 12 inches from the inflow, while they stimulated leaping in the smaller fish used in these experiments, caused the leaps to appear disorientated (p. 12). In the experiments, leaps which originated over twelve inches from the fall were not directed at the crest and were similar to those at the limit of distance (20 feet). In the Pot of Gartness, however, standing waves did not develop distant (relatively) from the zone of impact and the larger salmon made orientated, though unsuccessful, leaps from a distance of 20 feet; but in the absence of a visible standing wave leaps at 50 feet distance were made in all directions.

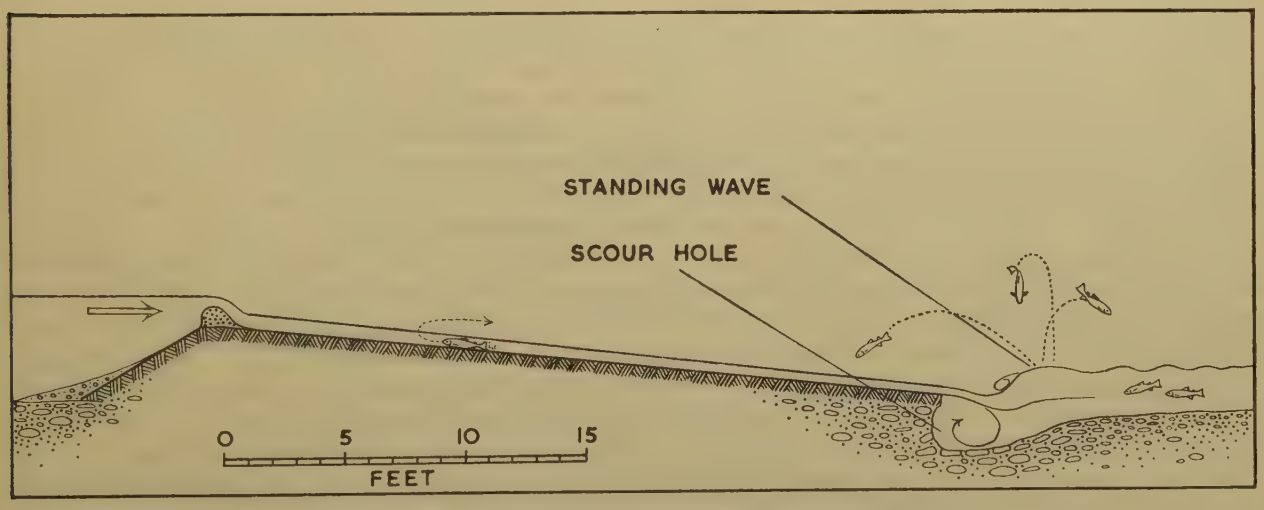

Fig. 12 Diagrammatic section through Trowmill Weir, R. Teviot.

Similar disorientated leaps can be seen at many broad, sloping weirs where the velocity is checked at the base by the formation of a standing wave. Fig. 12 illustrates a notorious weir on the River Teviot where salmon and trout at certain water levels invariably leap into the air from the crest of the standing

wave formed at the base over thirty feet distant from the crest of the weir. These leaps are, of course, abortive, and result in extensive damage to the fish which often strike the sloping platform with considerable force. During the autumn runs the impact made by a gravid fish frequently causes the ova to be shed involuntarily. The weir is passable only at relatively high water levels when damming effects downstream from the weir reduce the differences between upstream and downstream river levels and shorten the effective breadth of the weir. At low and normal flows that do not result in the formation of standing waves the water flowing over the weir is too shallow and its velocity too high to permit passage by swimming.

Physical Aspects of the Leap

The great amplitude of the flexion of the fishes' body, sometimes seen as it leaves the surface of the pool, suggests powerful strokes of the tail near the surface as the main source of propulsion through the air and the origin of the fanciful idea of the fish using its body as a spring by straining against the tail held in the mouth (p.4). Similar flexions of large amplitude are always seen as the female trout or salmon excavates her nest, when the powerful upward and downward strokes are capable of dislodging stones and gravel and depressing the surface of the water. During the 'cutting' act, the fish turns on her side and directs the force of these movements downwards and to the rear, but this very powerful effort results in little or no forward propulsion of her body. Examination of a large number of photographs of the same act performed throughout the whole course of nest building by many individual fish indicates its stereotyped nature and shows that in all cases, without exception, the pectoral and ventral fins are rigidly distended and extended headwards, thus resisting forward movement and directing the forces towards the gravel (Plate 5). On the other hand, the leaping fish as it leaves the water and travels through the air, having performed immediately previously flexions of the same order, does not show this rigid extension of the fins (Plate 6), and in the forward swimming fish these fins are closely applied to the body. There is here a clear example of two patterns of behaviour, variable in relation to separate external (and possibly internal) stimulation, superimposed on an invariable pattern of muscle activity (see Baerends, 1957). The amount of physical energy employed by the fish to move large quantities of gravel on the stream bed by displacement currents is probably available to propel the fish from the denser medium into the air. In general, the same muscular activity is involved and the energy utilised for the leaping act expended in one rapid outflow.*

While the eruption of the fish from the pool is generally obscured owing to its location at the centre of turbulence the subsequent journey through the air is more clearly defined and the trajectory of successive fish is relatively constant. As observed above, the success of an almost vertical leap depends on the ventral side of the fish striking the region of the crest of the fall first, followed by rapid submersion of the tail; in many cases where considerable velocity is encountered at this point it is essential that the tail should function as a propeller without delay. As we have seen, the orientation of the fish in its trajectory facilitates the attainment of the first condition and subsequent successful passage is dependent on channel gradient immediately upstream from the crest. If the channel slopes downwards in an upstream direction, as in normal pool topography, a very few strokes of the tail suffice to place the fish safely in deep water. In the experimental channel where the leap took the fish directly into deep water, the propulsive motion of the tail was still maintained to carry the fish a distance upstream before it checked its progress and swam directly to the bottom (p. 21). Some indication of the result of this initial impetus is seen in Plate 7 where the track of the submerged fish, which preceded the fish attaining the crest of the weir, at its extremity shows the effect on the surface of the pool of the change in direction.

At the Pot of Gartness where, instead of a deep pool upstream from the crest, the fish encountered a chute-like gradient, the initial impetus often enabled a fish to make progress against the high velocity current, or at least to maintain its position for a few seconds; it was, however, often defeated by the speed of flow.

*It should also be noted that these bursts of energy can be repeated in fairly quick succession. The salmon mentioned on page 27 which leapt a height of 7 feet 7 times in 15 minutes accomplished in effect within this time a compound vertical leap of approximately 50 feet.

A fish that leaps to the height of an obstacle in one directed movement thus enters unknown or unpredictable upstream conditions, equipped by its reflexes to counter, at least partly, high velocities beyond the crest. The body of the fish, once clear of the pool beneath, becomes projectile-like with a tail vibrating audibly and so rapidly that it appears as a blur to the human eye. The effect of these vibrations as the fish submerges at the crest cannot be doubted when it is seen to enter rapid flow, for it is already geared for immediate propulsion where the slightest delay in reaction would cause it to lose ground and be swept back over the fall. It was observed that every fish, once it entered the high velocity current, relaxed its efforts immediately it began to lose ground and was then swept backwards. On the other hand, these instinctive reactions were not modified in any way when the fish, after its leap, submerged into relatively tranquil, deep water and as a result was propelled unnecessarily far upstream. In the laboratory, the subjective impression was obtained of the fish becoming suddenly aware of its excessive speed and checking its forward movement at that moment.

In addition to the obvious advantage of the vibrating tail when the fish re-enters the water, there is also the possibility that the oscillations of the fin may assist the fish in maintaining a true line of flight and may perhaps also facilitate its propulsion through the air. Richardson (1936) describes an effect known to aeronautics as the Katzmayr effect which he considers pertinent to fish locomotion problems. The effect refers to the reduction of resistance sometimes experienced by an aerofoil when, instead of meeting the wind at a fixed angle of incidence it is given a periodic see-saw motion through a small angle. He states that theory shows that the reduction in the drag component will be most apparent when the object is such that the lift component (or cross-force) varies rapidly with angle of incidence, and may in some cases attain a negative value, so that the aerofoil actually propels itself against the stream. Richardson also states: 'Owing to the difficulty of seeing how to apply the Katzmayr effect to full scale aeronautics it has remained of merely academic interest, and an exact theory of the effect is not available. It seems, however, to be an effect which cannot be disregarded in reference to fish locomotion, although an actual fish differs from the aerofoil model in that it is not rigid, and cannot oscillate rigidly about an axis as in the aeronautical experiments . . . . The conditions of the experiments are however approximately fulfilled in the locomotion of those fishes whose bodies are too stiff to show a true sinusoidal motion, but merely flap to and fro, such as the mullet . . . .'

We have seen, however, that a salmon or a trout as it leaves the water, adopts a rigid posture with a vibrating tail which may approximate in effect to the described aerofoil model oscillating rigidly about an axis.

Downstream Migration

In the course of the present work on the ascent of migratory fish some observations were made on the complementary aspect of their return, and their progeny's migrations, downstream, which also produced evidence of the importance of vision to successful navigation. In concluding the present account of the investigations it is considered that a brief note of these observations will not be out of place as they may contribute to the overall efficiency of fish passes.

It had been noted during spawning runs that it was difficult to drive fish from certain pools into a net positioned at the outflow. In most other pools the fish shot into the net with little or no hesitation. It was also noted that spent fish tended to collect in the first type of pool and were seldom found in the second type. Other studies on the fate of fry during the slow drying up of a small stream during drought indicated that at very low and decreasing water levels pools of the first type eventually became death traps for the fry while the second type of pool was often vacated in good time.

Pool type 1 is characterised by deep water immediately upstream from the outflow caused by the presence of rock ledges or protruding tree roots, also by artificial dams made to divert water into lades. Type 2 has the typical profile of the spawning pool with the deepest part at the head or middle, the depth decreasing gradually as the bottom slopes upward to the outflow (Stuart, 1953a, 1953b, 1959). It was observed that the adult fish, when driven from end to end of the pools, maintained a constant distance from the bottom irrespective of varying depth, with the result that when they reached the end of a pool of type 1 they encountered the dam some distance below the overflow and then turned up-

stream again while maintaining the same swimming level. In pools of type 2 they continued downstream over the riffle even when it resulted in their almost complete emergence from the shallow water.

These pool types have been simulated in the laboratory tanks and in artificial channels outdoors and the results obtained from experiments conducted in them have confirmed the field observations and given some indication of the reactions which assist migratory fish to move downstream and of the problems of orientation and navigation.

In the laboratory, pools of various lengths were set up in the perspex channel by the insertion of perpendicular weirs, as in Fig. 1. Groups of 30 to 100 salmon parr and trout, 6 cm. to 20 cm. in length, were observed in pools which varied in length from 8 to 20 feet and were 9 in. deep. It was noted that the swimming distance, referred to the bottom, of the driven fish varied directly as the length of the fish and for a given size of fish was relatively constant, as noted in the field. It was not found possible to drive the fish over the spillways by any means except by handling them. When these observations were confirmed by repeated experiment, the contour of the bottom was altered by heaping mounds of gravel to form humps and depressions over which the fish were again driven. All sizes of fish behaved similarly. For convenience, the following description refers to a relatively uniform group of fish 10 cm. to 12 cm. in length.

For this group it was found that the swimming distance from the bottom was approximately 3 in. (7·5 cm.) and this distance was maintained closely over the humps and depressions except when the humps were separated by less than three times the length of the fish when there was a tendency to swim from peak to peak (Fig. 13A).

When a sheet of transparent perspex was laid across a depression between two humps and over three inches from the bottom the fish still tried to maintain the three inch distance from the visible bottom and 'stood on their heads' on the perspex in their attempts to do so. In the same manner the fish collided with another sheet inserted to form a ramp from bottom to crest of spillway and were often carried over by the current while attempting to regain the distance from the visible bottom (Fig. 13B).

The importance of vision in maintaining the relevant distance from the bottom was further demonstrated when the transparent sheet ramp was replaced by an opaque one. The fish no longer collided with the ramp but continued up towards the spillway maintaining the three inch swimming distance until space between the ramp and the surface of the water became constricted (Fig. 13C). The fish were now easily driven downstream from the pool.

The opaque sheet was then inserted an inch below the transparent sheet with the result that the fish in maintaining the three inch distance from the visible substratum brought their paths an inch closer to the transparent sheet. Further lowering of the opaque sheet while maintaining a parallel gradient beneath the transparent one eventually restored the conditions illustrated in Fig. 13B, when the fish again collided with the transparent sheet now more than three inches above the opaque sheet (Fig. 13D, E).

Concurrently with the laboratory experiments, similar results on a slightly larger scale were obtained in artificial pools situated in the laboratory grounds. In one of these larger pools thirty-two trout between 16 cm. and 20 cm. in length remained for 18 months with only the loss of one fish into the pool below although no grid was inserted to prevent egress.

An eighteen inch high weir of boards proved to be an adequate barrier over which it was usually impossible to drive the fish even when panic reactions resulted from the effort. On the other hand, the insertion of a solid or louvred ramp permitted the evacuation by driving of all the fish within a period of twenty minutes or so (the last few fish always being responsible for the delay). When the ramp was inserted quietly and the fish left peaceably alone a large proportion filtered daily over the weir into the pool below. Table 3 summarises the results over periods of six consecutive days and of four periods each of three days, when the fish were allowed to accumulate in the lower pool. The fish were barred from upstream movement. It is interesting to note, however, that it was not found possible completely to evacuate the pool over an extended period of time and three or four fish always remained in the pool over periods of several weeks even at the season when downstream migration was in evidence in the field. No explanation can be given at present for this reluctance though it has already been shown that not all individuals of a trout population move downstream with the majority (Stuart, 1957); there may also be a connexion with the territorial behaviour described on page 21.

Evidence is accumulating to indicate that the building of high dams for hydro-electric power is

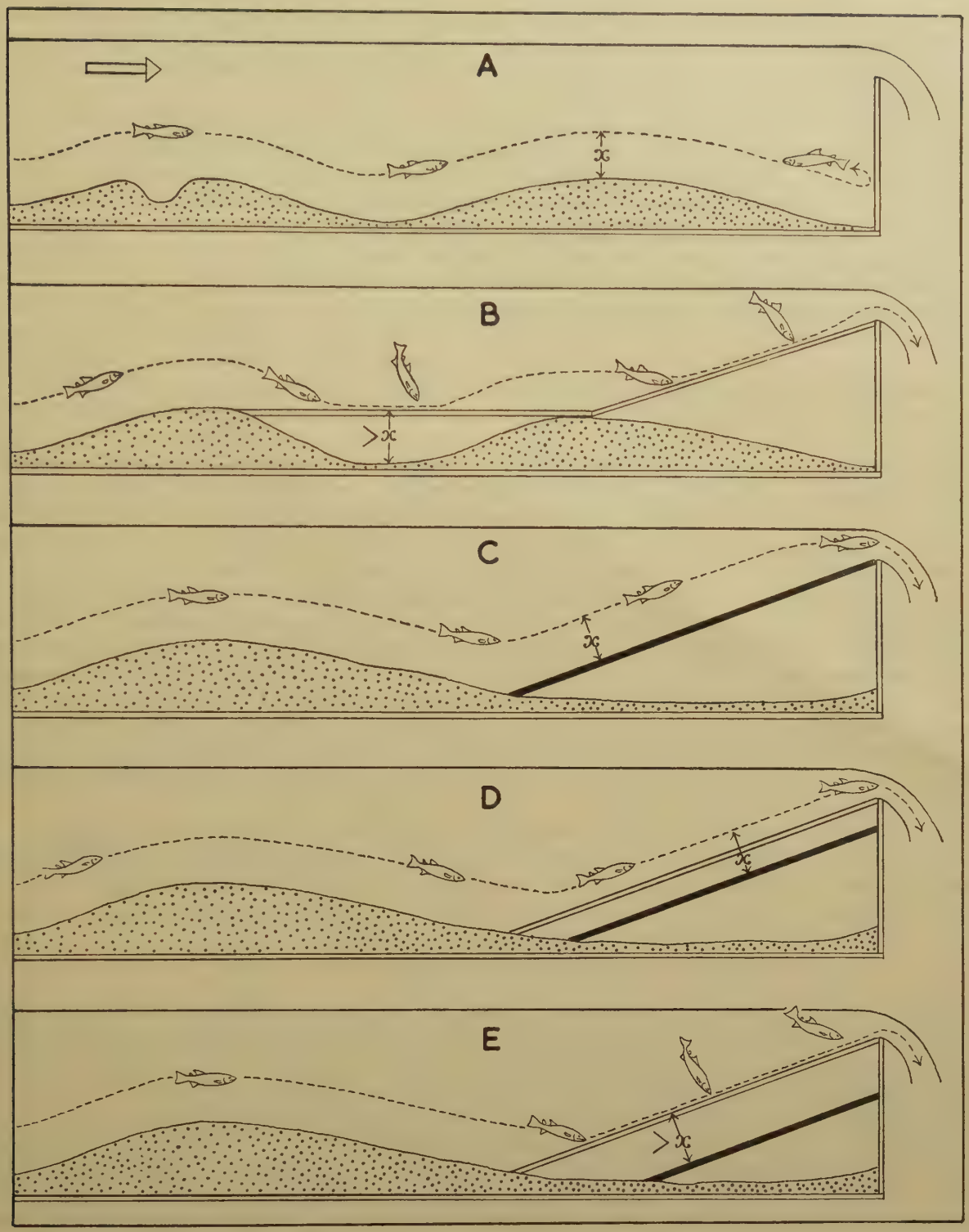

Fig. 13 The reactions of salmonids to the visible substratum and to transparent and opaque ramps leading to outflow.

delaying the passage of salmon smolts beyond the time of normal migration. In the resulting reservoirs various devices have had to be considered in attempts to prevent egress of the fish by way of the turbines where physical damage to the fish could result. Egress over sloping spillways has also been shown to result in abrasion with high mortality.

On passage through deep reservoirs, pools and estuaries, salmon smolts tend to migrate in the surface layers where they may be observed in shoals moving downstream tail first in the slowly moving currents. In broad, deep waters beyond visual contact with the bottom they are thus entrained by the current and conducted to the main outlet which in hydro-electric reservoirs is normally the intake to the turbines from which they are generally barred for the reason given above.

The designed fish way is usually situated at a distance from the turbine inlets, often on the opposite side of the dam or in the centre and draws a lesser current to its opening on the steep face of the dam. In the absence of adequate guiding stimuli, in competition with the attraction of the greater volume of water passing to the turbines, many fish may find the fishway only by chance and this is probably one of the principal causes of delay. Location of the fishway is, however, not always followed by its immediate acceptance by the fish and shoals of smolts have been observed radially disposed several feet in front of the entrance swimming against the accelerating and converging currents which would otherwise have carried them safely out of the reservoir.

The normal negative rheotaxis of the downstream migrant is thus not exhibited under these conditions over deep water although an entrained fish trapped in a stronger current will rapidly reorientate its body at the moment of reaching the lip of the spillway and so pass downwards head first. It therefore seems likely that the reluctance of the fish to pass out of a reservoir through the equivalent of a gap in the almost perpendicular wall of the dam is related to the absence of a visible substratum or lack of direct contact with the bottom without which normal orientation is impossible (Fraenkel and Gunn, 1940). The remedy may perhaps be found in the provision of a false substratum which will permit the optical responses on which orientation depends e.g. the apparatus described above in the form of a ramp. Later experiments have shown that the false substratum need not be of solid construction and that a light framework of laths constructed of wood or metal is readily accepted by the fish. The provision of adequate space between the horizontal laths permits the upward passage towards the light of any fish which should approach from beneath as well as reducing the weight of the apparatus. In a deep reservoir the lower end of the ramp need not extend downwards beyond the range of visibility of the fish and probably a depth of eight to ten feet would suffice.

Large scale field experiments would be necessary to decide if advantage could be taken of the attraction of the major current towards the turbines to permit the location of the fishway immediately above such intakes with an inclined louvred ramp to guide the surface swimming migrants towards a more natural exit.

CONCLUSIONS

The results of the above experiments have shown that the impact of falling water attracts the fish towards the site of the fall. In the river, the force of the impact varies with the discharge and the amount of air entrained and possibly explains why leaping is in evidence at certain times and not at others, as well as the segregation and differing behaviour of the fish according to size. The choice of route, which is not constant for any size range, may also be dependant on the nature of the impact.

In the absence of a standing wave the fish will endeavour to swim over the obstruction, which, if it approaches the perpendicular, or if the velocity of the water is too great, leads to abortive effort. If the standing wave is located distant from the crest of the fall beyond the visual range of the fish, as is found below a chute or long sloping weir, the leaps may not be orientated and the effort is again wasted. Where, however, the fall is vertical, or nearly so, and the scour hole beneath has attained stable dimensions, the standing wave becomes located at the nearest possible point to the crest of the fall, the leap becomes orientated towards the crest, the trajectory of the leap becomes steeper and shorter and the fish, even if the assistance from the upward currents of the submerged vortices is considered negligible, does not have to contend with adverse velocities.

The importance of the visual stimulus has become evident from the above experiments, particularly in respect to orientation to the crest of the fall and to the inhibition of leaping during darkness. It is hoped to undertake further investigations in this direction especially in relation to other types of fish passes, notably those that make use of fish locks where the entrances are subject to low light intensity, particularly at certain periods during the day.

It is also possible that the above observations give a hint of the limits of the vision of the fish in air and it is hoped that further investigations will add to our knowledge in this respect. It is not, however, to be expected that a submerged fish in the turbulence generated below the fall could make any estimate of the height or presence of an obstruction as this would imply the making of an allowance for the difference in refraction of air and water, even through water surfaces undisturbed by turbulence and unobscured by foam. This alone should have been sufficient to arouse doubts regarding earlier theories which postulated a fast approach run from a depth below the surface. According to Brett (1957), the vision of objects in air is greatly restricted below a depth of a few metres even when the surface is relatively undisturbed by wave action.

There can be little doubt, from the evidence already obtained, that the fish must emerge partly from the water before orientating its body for the leap over a fall, and if the obstruction is a visible one it appears able to coordinate its movements to launch its body in the proper direction. If the obstacle is not within its range of vision owing to its distance, or is perhaps invisible, as in a standing wave barrier, the leaping which is stimulated by the disturbance is not orientated; if visibility is reduced owing to darkness (or lack of contrast between the boundary of the obstruction and the background) the leaping stops. The writer has never seen a fish attempt to leap up a fall in relative darkness and has been present on numerous occasions when leaping ceased abruptly, after a period of great activity, with a marked diminution in daylight. These observations are in accordance with the findings of Denil (1938) and also of Brett and Mackinnon (1954) who investigated the hourly rate of migration of adult coho and spring salmon (*Oncorhynchus kisutch* and *O. tshawytscha*) ascending a fish ladder and found that the run varied from one to two peaks during daylight hours to zero at night.

Fishways should, logically, be equally effective for upstream and downstream migrants. It has been shown that the scour hole produced under experimental conditions (Fig. 5) in the study of upstream migration effectively altered the artificial contour of the pool to produce a 'ramp' of gravel which we have seen is of considerable assistance to the reversed movement. Fish ladders designed on these principles are likely, therefore, to satisfy both requirements.

In such designs there is the further advantage of there being no possibility of the individual pools becoming blocked with silt or gravel because the current would continue to transport the entrained material through each pool. If however, for reasons of economy a modified design omitting the ramp should be employed accumulations of gravel and silt would conform to the space which otherwise would have been occupied by the ramp. The effect of this would be beneficial as the deposits would restore the conditions necessary for laminar or non-turbulent flow into the succeeding pool. In passes built at high dams, however, it is unlikely that gravel would enter and the ramp should not be omitted. In this connexion it may be observed that even in high dams the 'ramp' would become restored in the reservoir in course of time in the absence of management, by accumulations of mud and silt.

Finally it should perhaps be emphasised that recommendations regarding the design of fishways that emerge as a result of these investigations are reinforced by the fact that such 'designs' are established as natural phenomena in all channels in which water flows. It may therefore be reasonable to assume that the fishes are more closely adapted to the resultant hydraulic conditions than to any innovations which have no natural counterpart in rivers and streams which support stocks of salmon and trout.

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My thanks are also due to Mr. D. H. Mills for the photograph reproduced as Plate 7.

SUMMARY

1. Laboratory and field observations and experiments have shown that the behaviour of migrating salmonids, adult and juvenile, when faced with a barrier or obstruction, can be correlated directly with the hydraulic conditions obtaining in the river channel.

2. It is probable that the signal that stimulates the fish to move forward preparatory to the leap over an obstacle is related to the impact of falling water on the surface of a pool. As the force of the impact varied with changing discharge so also did the relative size of the fish that responded. The response also varied with the amount of air entrained in the water.

3. The stimulus to leap was found to be closely related to the presence of a standing wave (or hydraulic jump) and the location of the standing wave distant to the obstacle influenced the success of the leap. Thus in shallow fall pools and pools below sloping weirs the standing wave becomes located too far downstream for the fish to strike the crest of the fall on the upward arc of its trajectory. If the fish strikes the falling water on the downward arc it is immediately swept downstream. Optimum leaping conditions were obtained when the depth of the fall pool was increased so that the standing wave became submerged at the 'toe' of the fall, the ideal ratio of height of fall to depth of pool being 1 : 1·25.

4. All leaps in the laboratory and in the field were observed to be initiated at the surface of the pool (on the neutral point of the standing wave) and no fish was observed to approach in a run from a distance, laterally or vertically, and perform a leap without a halt near the surface of the pool.

5. The great amplitude of the flexions of the fishes' body as it leaves the surface of the pool suggests powerful strokes of the tail near the surface as the main source of propulsion through the air. This action is compared to the effort expended by the nest-building female whose powerful body flexions, by displacement currents, excavate the gravel in the river bed.

6. The importance of the visual stimulus in relation to varying heights of obstacles and the orientation of the leap has been demonstrated. Fish that are stimulated to leap by a standing wave located at a distance from the crest of a weir or waterfall which exceeds their visual range perform unorientated leaps and all leaping activity ceases at low light intensities.

7. The problem of the passage of migratory salmonids over artificial obstructions is discussed and experiments are described which suggest that the provision of the normal contours of a natural river channel bed would facilitate the passage of both upstream and downstream migrants by reproducing hydraulic phenomena to which they are manifestly adapted.

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TABLE 1

Consecutive Leaps up Adherent Nappe—Mixed Groups

Attempt No.	Series 1	Series 2	Series 3
1	M	M	MM
2	MM	M*	MM
3	M	S	S
4	MS*	M	MS
5	S	S	SM*
6	M*	MS	M
7	S*	MM	M
8	S	S	M
9	M	S	MM
10	S	MM	M
11	M	M	M
12	MMM	M	MS
13	MM	M	S*
14	S	S	MM
15	MM*	MM	S
16	MS	MM*	M
17	MM	M	MS
18	S	M	MM
19	MM	M	M
20	M	MM	MM
	M21:S8	M20:S6	M23:S7

M—minnow; S—salmonid
MM, MS etc.—coincident leaps
M*, S*—successful attempts

TABLE 2

Analysis of Successful Efforts—Homogeneous Groups

No. of Leaps	No. of Successful Attempts											
	Minnow Series				Parr Series				Trout Series			
	1	2	3	4	1	2	3	4	1	2	3	4
1					1		1	1		1	1	1
2									1			
3		1			1							
4						1		1	1	1	1	
5												1
6				1								
7	1					1	1					
8												
9									1			1
10											1	
11	1	1	1									
12							1	1		1		
13						1						
14				1	1							1
15		1										
16											1	
17												
18								1				
19						1			1			
20						1				1		1
Totals	2	3	1	2	3	5	3	4	4	4	4	5

TABLE 3

Evacuation of Ramped Pool over periods of Six Consecutive Days and over Four periods, each of Three Days

	No. of Fish Leaving Pool	Percentage of Total (32)
Consecutive Days		
1	19	59
2	17	53
3	12	37
4	21	65
5	20	62
6	18	55
Three-Day Periods		
1	29	90
2	25	77
3	25	77
4	28	87

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